

Sedimentological characteristics and paleoenvironmental implication of Triassic vertebrate localities in Villány (Villány Hills, Southern Hungary)

GÁBOR BOTFALVAI^{1,2,✉}, ORSOLYA GYŐRI³, EMÍLIA POZSGAI⁴, IZABELLA M. FARKAS⁵, TAMÁS SÁGI^{6,7}, MÁRTON SZABÓ^{1,2} and ATTILA ŐSI²

¹Department of Paleontology and Geology, Hungarian Natural History Museum, Baross Street 13, H-1088, Budapest, Hungary; botfalvai.gabor@gmail.com

²Department of Paleontology, Eötvös Loránd University, Pázmány Péter sétány 1/C, H-1117, Budapest, Hungary; szabo.marton.pisces@gmail.com, hungaros@gmail.com

³MTA–ELTE Geological, Geophysical and Space Science Research Group, Pázmány Péter sétány 1/c, H-1117 Budapest, Hungary; gyori.orsi@gmail.com

⁴Soós Ernő Water Technology Research and Development Center, University of Pannonia, Zrínyi Miklós Street 18, H-8800 Nagykanizsa, Hungary; emily.pozsgai@gmail.com

⁵Laboratories MOL, MOL Plc., Szent István Street 14, H-1039, Budapest, Hungary; izabella.farkas@gmail.com

⁶Department of Petrology and Geochemistry, Eötvös Loránd University, Pázmány Péter sétány 1/C, H-1117, Budapest, Hungary; sagi.tamas@ttk.elte.hu

⁷MTA-ELTE Volcanology Research Group, Pázmány Péter sétány 1/C, H-1117, Budapest, Hungary

(Manuscript received September 26, 2018; accepted in revised form February 12, 2019)

Abstract: There are two Triassic vertebrate sites in Villány Hills (Southern Hungary), where productive and continuous excavations have been carried out in the last six years resulting in a rich and diversified assemblage of shallow marine to coastal animals. The studied formations belong to the Villány–Bihor Unit of the Tisza Megaunit, which was located at the passive margin of the European Plate during the Triassic. The relatively diverse vertebrate assemblage was collected from a Road-cut on Templom Hill and a newly discovered site at a construction zone located on the Somssich Hill. Four main lithofacies were identified and interpreted in the newly discovered Construction vertebrate site consisting of dolomite (deposited in a shallow, restricted lagoon environment), dolomarl (shallow marine sediments with enhanced terrigenous input), reddish silty claystone (paleosol) and sandstone (terrigenous provenance) indicating that the sediments of the Construction vertebrate site were formed in a subtidal to peritidal zone of the inner ramp environment, where the main controlling factor of the alternating sedimentation was the climate change. However, the recurring paleosol formation in the middle part of the section also indicates a rapid sea-level fall when the marine sediments were repeatedly exposed to subaerial conditions. In the Road-cut site the siliciclastic sediments of the Mészhegy Sandstone Formation are exposed, representing a nearshore, shallow marine environment characterized by high siliciclastic input from the mainland.

Keywords: cyclic carbonate–siliciclastic deposits, dolomite, inner ramp, peritidal zone, vertebrates, Tisza Megaunit.

Introduction

The vertebrate remains from the Mesozoic of Hungary are relatively rare, and aside from a few isolated fossils only three localities are known where productive and continuous excavations have been conducted. Two of them provide vertebrate fossils from Upper Cretaceous strata (Ajka and Csehbánya Formations), deposited in freshwater and terrestrial environments. Fishes, amphibians, turtles, crocodiles and dinosaurs were found in these sites of the Bakony Mountains (Ősi et al. 2012). The third vertebrate locality is situated in Villány, Villány Hills (South Hungary) and includes two outcrops of the Middle to Upper Triassic formations (Fig. 1). Field work in these sites revealed rich and diverse assemblage of coastal to shallow marine animals including scales and teeth of fishes, cranial and postcranial elements of sauropterygians (notho-

sauurs and placodonts), and vertebrae of *Tanystropheus* (Ősi et al. 2013; Segesdi et al. 2017; Table 1). These Triassic fossils and their embedding successions are of great importance, since according to the relevant paleoreconstructions the Tisza Megaunit, and within it the Villány area, was located at the Northern Neotethys margin, on the shelf of the European Plate southwards to the Bohemian Massif (Csontos & Vörös 2004; Haas & Péro 2004; Pozsgai et al. 2017).

Middle to Late Triassic marine to coastal vertebrate fossil sites are well known from the Central European Basin and Alpine successions representing the Western European realm of the Tethys (e.g., Pinna 1990; Rieppel 2000; Schoch 2015; Renesto & Dalla Vecchia 2018). However, much less is known about the vertebrate faunal composition of the eastern regions of the Northern Tethyan coast. With its abundant and relatively diverse fauna (chondrichthyans, osteichthyans, nothosaurs,

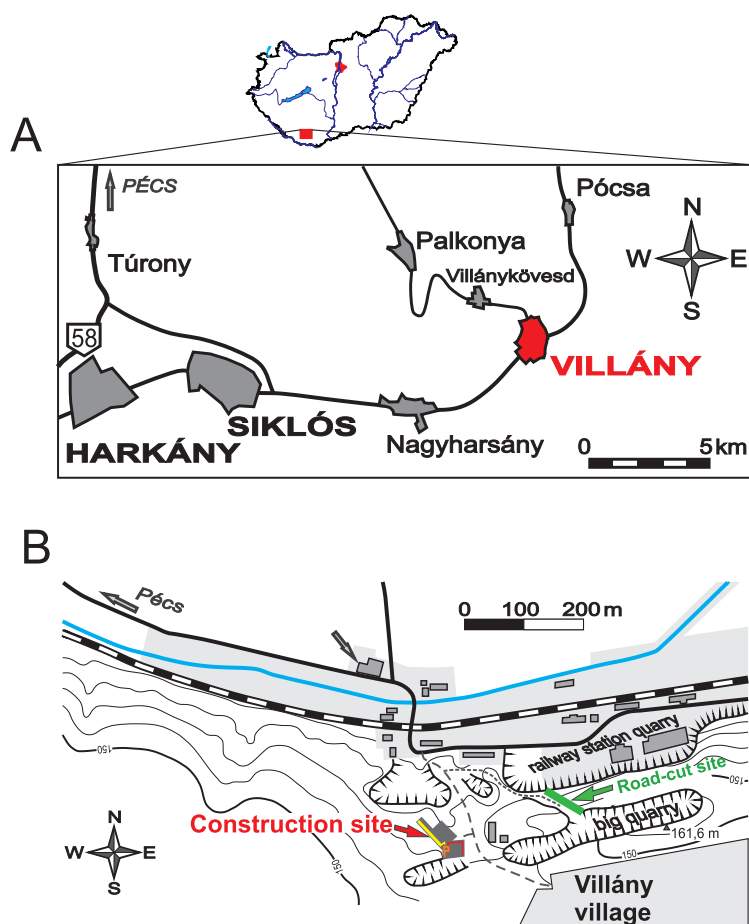


Fig. 1. Map of the locality (A) and location of the two vertebrate sites in Villány (B).

placodonts, archosauromorphs) is thus of great importance since it extends our geographic and faunistic knowledge on the shallow marine to seashore vertebrates of the Northern Tethyan coast.

Besides the paleogeographic uniqueness, the vertebrate fossils of the Villány sites help to gain a better understanding of the Late Ladinian to Early Carnian evolutionary events of sauropterygian and prolacertiform archosauromorphs, since the record of these groups from this period of the Triassic is much less known than from earlier periods. Thus, a detailed evaluation of the sedimentological features and reconstruction of the depositional environment of these recently discovered bone-yielding beds are crucial in the paleoenvironmental reconstruction, which is indispensable for the upcoming paleontological research. Furthermore, besides the paleontological significances, the explored successions provide additional information about these sedimentological and environmental processes. The bone-bearing successions of the Villány Hills were deposited in an inner ramp environment (Rálsch-Felgenhauer & Török 1993; Török 2000, and see below) representing the transition zone between the upper shoreface and fair-weather wave base (Burchette & Wright 1992). Mixed siliciclastic-carbonate deposits frequently accommodate in such environments consisting of both

extrabasinal (e.g., terrigenous siliciclastic) and intrabasinal (autochthonous carbonate) components (Morsilli et al. 2012; Caracciolo et al. 2013; Chiarella et al. 2017). The alternation of lithofacies and/or the sediment mixing can be interpreted as the result of short-term sea-level or short-term climate changes. Thus, the investigation of this type of successions is useful to understand short-term sea-level and climatic changes and processes (e.g., Brachert et al. 2003; Zeller et al. 2015; Blanchard et al. 2016; Reis & Suss 2016).

The sedimentological characteristics of one of the vertebrate sites (Road-cut section) is well documented by several authors (Rálsch-Felgenhauer 1985; Vörös 2009, 2010), but the interpretation of the depositional environment of this succession remained controversial. We performed here new observations and paleontological data, which may help to determine the depositional environment of this sediment accumulation. The other bone-bearing excavation site (Construction site) is less studied, because detailed paleontological and sedimentological investigations of this succession has started only in 2012, when the section was industrially excavated, and one of the authors (E. Pozsgai) found a few bones and teeth in this section and the area was recognized as a potential Triassic vertebrate locality.

The aim of the present study is to give an insight into the sedimentological history of the bone-yielding successions. Based on the detailed description and interpretation of the identified facies associations, the sedimentological and geological significances of the shallow marine setting are discussed, and the depositional paleoenvironments of the vertebrate sites are identified.

Location and regional geology

The Villány Hills are situated in the southwestern part of the Pannonian Basin in Hungary (Fig. 1A). The studied successions are located 200–300 m northwest to the city of Villány (Fig. 1B). The Villány Hills belong to the Villány-Bihar Unit of the Tisza Megaunit, which formed a segment of the passive Neotethys margin of the European Plate during the Triassic (Csontos & Vörös 2004; Haas & Péró 2004; Feist-Burkhardt et al. 2008; Fig. 2A).

The Lower Triassic sequence of the Villány-Bihar Unit is predominantly characterized by clastic sediments (Buntsandstein facies), which is overlain by Middle Triassic evaporitic carbonate and shallow marine carbonate deposits (Röt and Muschelkalk facies). These sequences show a close genetic affinity with the Germanic-type Triassic sediments (Török 1997), while the Upper Triassic succession shows closer affinities to the Carpathian Keuper facies (Bleahu et al. 1994).

Table 1: Synthetic faunal list of the Triassic marine vertebrate fauna from the Villány Hills (based on Ősi et al. 2013; Segesdi et al. 2017 and Electronic supplement II).

Vertebrate assemblage		Construction site		Road-cut section		Lifestyle	
Taxon		Ladinian (Templomhegy Member)	Carnian (Mészhegy Sandstone Formation)	Ladinian (Templomhegy Member)	Carnian (Mészhegy Sandstone Formation)	Environment	References
Fishes	<i>Hybodus</i> sp.				×	marine, brackish, freshwater	Cuny 2012; Klug et al. 2010
	<i>Palaeobates angustissimus</i>	×			×	marine	Böttcher 2015; Diedrich 2009
	<i>Polyacrodus</i> sp.				×	marine	Diedrich 2009
	<i>Lissodus</i> sp.	×			×	marine, freshwater	Cappetta 2012
	<i>Gyrolepis</i> sp.	×			×	marine	Lakin et al. 2016;
	<i>Severnichthys acuminatus</i>	×			×	marine	Whiteside et al. 2016
	<i>Actinopterygii</i> indet.	×			×	marine, brackish, freshwater	Nelson 2006
Reptiles	<i>Nothosaurus</i> sp. 1	×		×		marine	Rieppel 2000
	<i>Nothosaurus</i> sp. 2	×		×		marine	Rieppel 2000
	cf. <i>Cyamodus</i> sp.	×				marine	Rieppel 2000
	<i>Tanystropheus</i> sp.	×				marine to coastal	Renesto 2005
	?Archosauriformes indet.				×	coastal to terrestrial?	

The Middle Triassic sequence was deposited on a homoclinal carbonate ramp of relatively uniform subsidence rate (Török 1997, 2000). The geotectonic setting and the related slow subsidence suggest that the sediment deposition may have been primarily controlled by the eustatic sea-level changes (Török 2000). In accordance with sea-level fluctuations, three Middle Triassic deepening-upward and shallowing-upward cycles were identified (Török 2000; Götz et al. 2003; Götz & Török 2008).

The first cycle corresponds to the ramp initialisation and the onset of carbonate sedimentation, coinciding with the Early Anisian global sea-level rise (Török 2000; Götz & Török 2008). The beginning of the transgressive phase of that cycle is represented by evaporitic sabkha sediments: dolomite, dolomarl and anhydrite (Hetvehely Anhydrite Formation; Fig. 2B). The following regressive phase is characterized by thick-bedded massive dolomite (Rókahegy Dolomite Formation).

The second depositional cycle took place during the Middle to Late Anisian period. It shows striking similarities with the first Muschelkalk cycle of the Central European Basin (Török 2000; Götz & Török 2008). The dark grey, nodular, fossiliferous clayey limestone (lower part of the Zuhány Limestone Formation; Fig. 2B) represents the transgressive phase (Götz et al. 2003), whereas the dolomitic limestones and the entirely dolomitized inner ramp carbonates (upper part of the Zuhány Formation) indicate the regressive phase of this cycle (Haas 2001). The latest Anisian to Early Ladinian interval is poorly documented in the Villány Hills. However, from the early part of the Ladinian the general shallowing of the basin can be assumed that is represented by yellowish grey dolomite with dolomitic marl intercalations (Csukma Dolomite Formation; Haas 2001).

The lower part of Csukma Dolomite Formation, known from outcrops and boreholes in the middle part of the Villány Hills, consists of grey, thick-bedded, locally laminated dolomites with rare relicts of ooids, micro-tepee and fenestral

structures (Török 2000). Based on sedimentological characteristics (e.g., presence of fenestral laminae, extensive dolomitization, tepees and exposure surfaces), the subtidal to peritidal zone of the inner ramp was interpreted as the depositional environment of the Csukma Dolomite (Rálich-Felgenhauer & Török 1993; Török 2000; Fig. 2B).

The uppermost part of the Csukma Dolomite, which is made up by the alternation of yellowish grey dolomite and dolomarl layers, was defined as the Templomhegy Dolomite Member of this formation (Fig. 3).

Remains of a relatively diverse marine fish and reptile fauna (Ősi et al. 2013) were recently encountered in this member (Construction site; see below). Unfortunately, only a few badly preserved casts of hard-shelled invertebrate fossils are known from the dolomite and dolomarl beds of the Templomhegy Member, which cannot be used for more detailed paleo-environmental reconstruction. However, a protected inner ramp lagoon and connected tidal flat were interpreted as the depositional environment of the Templomhegy Member (Török 1998, 2000; Haas 2001; Bérczi-Makk et al. 2004; Ősi et al. 2013).

The age of the Templomhegy Dolomite Member of the Csukma Dolomite Formation (including the bone-bearing horizon of Construction site) is problematic since index fossils of ammonites and conodonts are absent in this shallow marine sequence. However, the Templomhegy Dolomite Member probably belongs to the Ladinian stage based on its stratigraphic position, because it is situated between the Late Anisian Zuhány Limestone Formation and the Carnian Mészhegy Sandstone Formation (Rálich-Felgenhauer & Török 1993; Török 1998; Haas 2001; Fig. 2B). Furthermore, the new vertebrate material (especially the remains of *Nothosaurus* sp.), discovered from the Templomhegy Dolomite Member, also suggests a late Middle Triassic (Ladinian) age for this deposition (Ősi et al. 2013).

The relatively thick shallow marine Middle Triassic carbonate succession is overlain by a thin formation that is made up

mostly of siliciclastic rocks. It was defined as the Mészhegy Sandstone Formation and was assigned to the Upper Triassic (Fig. 2B). The Mészhegy Sandstone Formation (Fig. 2B) is composed of conglomerate, siltstone, sandstone, cellular dolomitic limestone and marl (Rálich-Felgenhauer & Török 1993;

Vörös 2009, 2010). The sedimentology of the Mészhegy Formation exposed in the Road-cut section is well documented, however, the depositional environment of this succession has been interpreted in different ways. Some authors argued that it is a shallow marine or littoral deposit (Rálich-Felgenhauer 1985; Török 1998), whereas Vörös (2010) claimed fluvio-lacustrine origin. The palynological investigation indicates a Carnian age for the lower part of the formation (Ősi et al. 2013 and see below), but the age of the upper part is still unknown. Vörös (2009) suggests that this formation is composed of three sedimentary parasequences, one definitely Carnian, and two others, possibly Norian and Rhaetian in age. However, this hypothesis is not supported by paleontological data due to the lack of age-constraining flora and fauna in the upper beds. The discovered fish remains show a uniform taxonomical distribution through the exposed section (see below), probably indicating a shorter depositional time for this formation (see below). The thinness (up to 20 m) of the formation and the seemingly continuous succession, as well as the available paleontological data rather suggest a Carnian age for the whole formation (Ősi et al. 2013).

The Mészhegy Sandstone Formation of the Road-cut site on Templom Hill is covered by the Pliensbachian Somssichhegy Limestone Formation. The lowermost yellowish sandstone strata of the Pliensbachian Somssichhegy Limestone Formation unconformably overlies the Triassic strata of the Mészhegy Formation (Vörös 1972, 2009, 2010, 2012).

Methods of investigations

The sedimentology of two Triassic vertebrate sites has been investigated in detail at Villány Hills (Fig 1B). Sedimentary rocks were analysed in the field and by hand specimens (1 kg from every layers), collected from both sections. The detailed field investigations included the determination of grain size, colour, bedding morphology along with recording of paleontological data.

For microvertebrate faunal investigations, samples were taken from three productive beds (L3–4–5) of the Mészhegy Sandstone Formation at the *Road-cut site*,

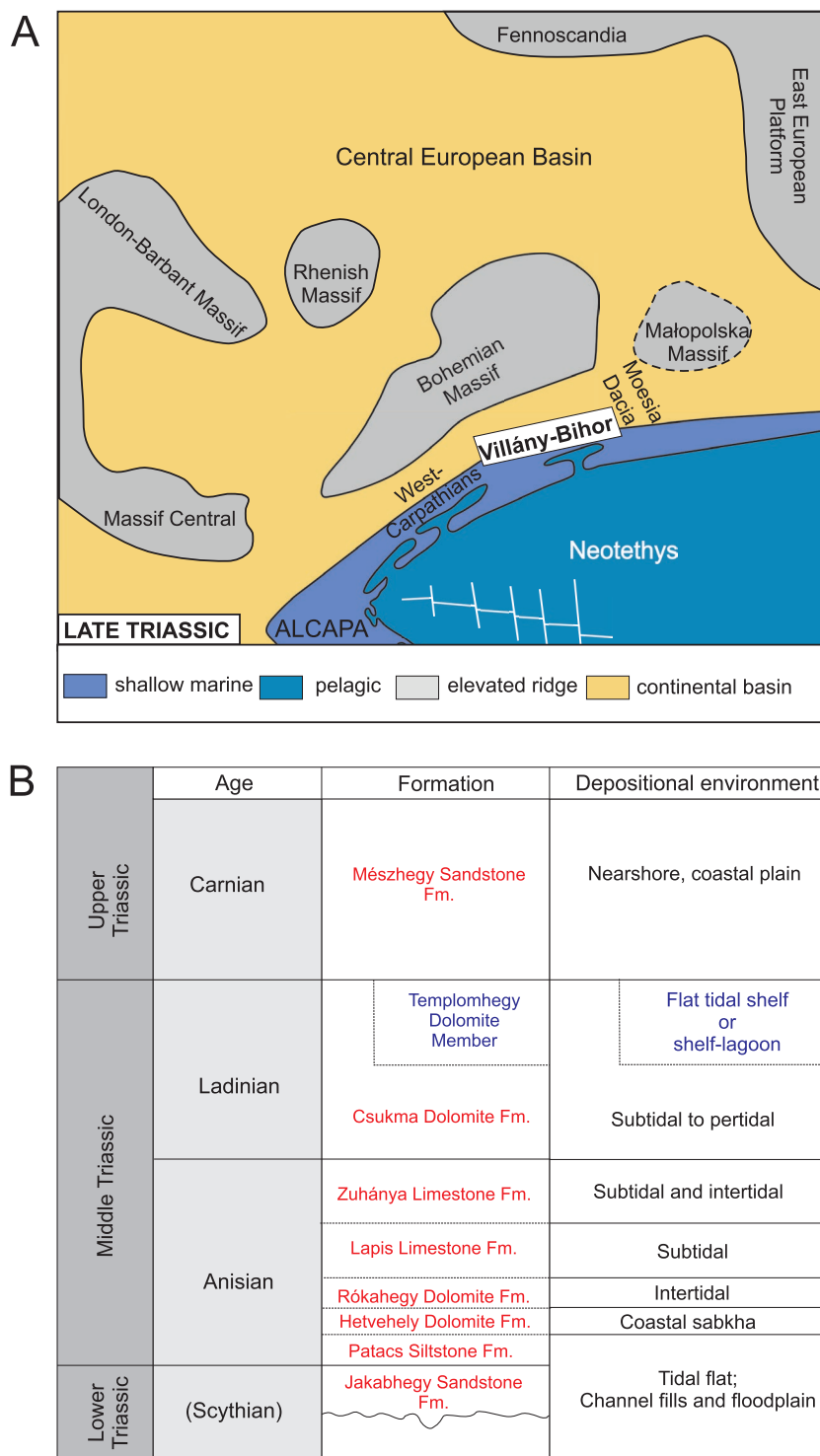


Fig. 2. A — Paleogeographical map of the Tisza Megaunit in the Late Triassic (compiled by Pozsgai et al. 2017). **B** — Triassic formations of the Tisza Megaunit (after Török 1998; Haas 2001).

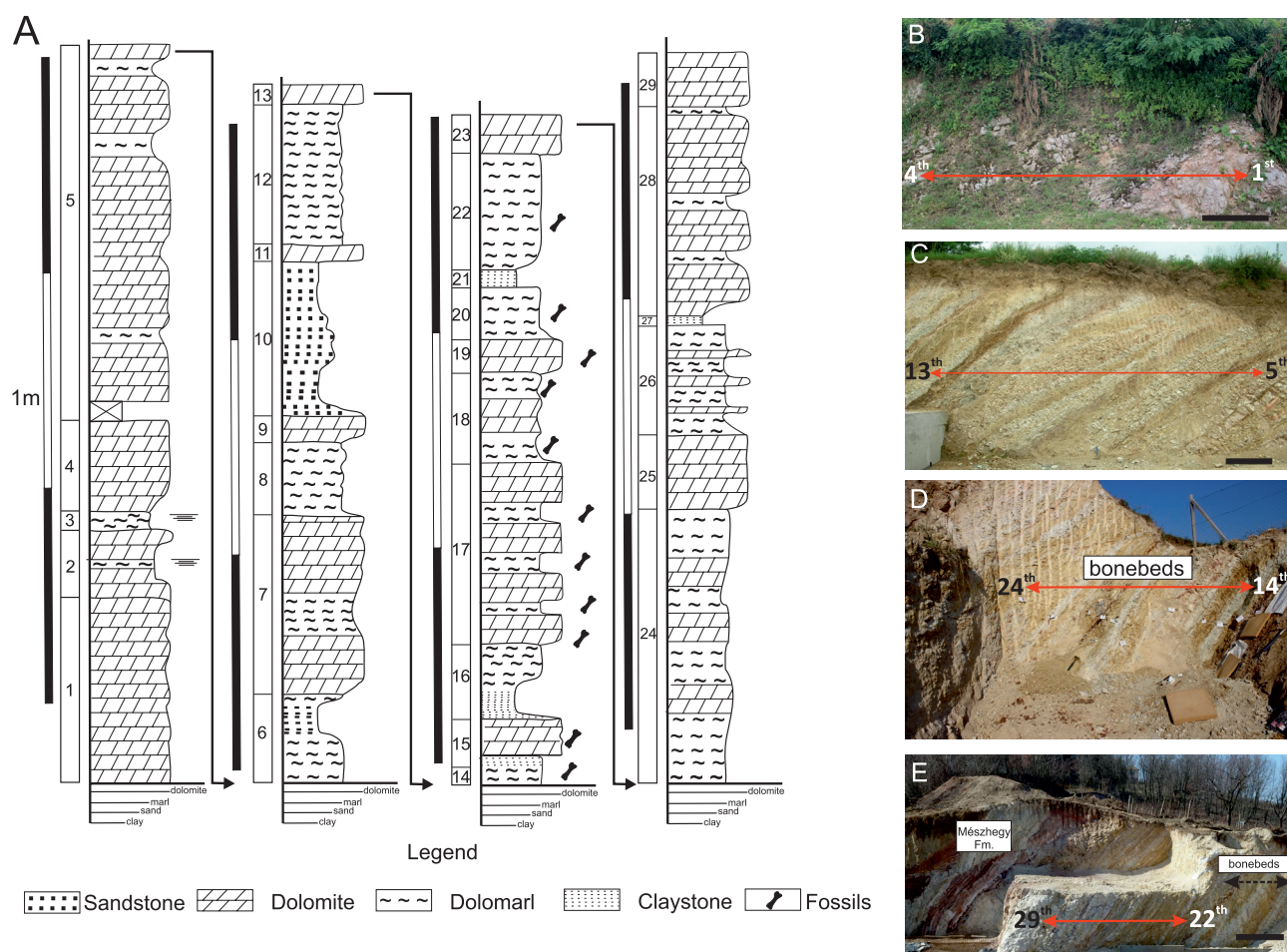


Fig. 3. Schematic stratigraphic section of the Construction site (A). The lower part of the observed section is made up by dominantly micritic dolomite beds with subordinate argillaceous deposits (B–C). There are main bone-bearing horizons of the Construction site (D). The bone-bearing succession is covered by 3 meter thick massive dolomite succession with thin dolomarl intercalations (E). The scale bars represent 1 m.

and four productive layers (14th, 18th, 20th and 22th layers) of the Templomhegy Dolomite Member at the *Construction site* (see below). The samples were screen-washed, by using tap water and 5 % of acetic acid. The dried residue was sorted under magnification, using a binocular microscope. The pictures from the material were carried out with a Hitachi S-2600N scanning electron microscope at the Department of Botany, Hungarian Natural History Museum (NHMUS).

Detailed petrographic investigations were carried out on 22 thin sections, prepared at the Department of Physical and Applied Geology, Eötvös Loránd University (ELU). A solution of alizarin red-S and potassium ferricyanide was used to identify the carbonate phases in the samples (Dickson 1966).

The X-ray powder diffraction (XRD) measurements were made using a Bruker D8 Advance powder diffractometer, with parallel beam, 2θ – θ geometry equipped with LynxEye® 1D detector. Before measurements the few grams, needed for X-ray analysis were grounded as fine powder with a mean diameter size between 1–5 μm using micronizing mill (Retsch MM 400 type) for 3+2 minutes. The final grain size was

obtained using agate mortar and pestle. The measuring parameters were: step-scanning at 0.01 $^\circ 2\theta$ intervals, counting time of 17.7 s (0.1). CuK α radiation at 40 kV and 40 mA was used. The measurement range was 2–70 $^\circ 2\theta$.

The identification of minerals was achieved using the Diffrac EVA software by comparison of the X-ray diffraction pattern from the sample with the International Centre for Diffraction Data PDF-2, release 2009 database. The (semi)-quantitative data were obtained using TOPAS software providing us a standardless quantitative analysis (based on Rietveld method).

Petrographic descriptions of the bed 10 were carried out with a Nikon YS2-T polarizing microscope and an AMRAY 1830 I/T6 Scanning Electron Microscope (equipped with a PU9800 EDX spectrometer) at the Department of Petrology and Geochemistry, ELU. Accelerating voltage of the SEM instrument was 20 kV with an average beam current of 1 nA. Back Scattered Electron (BSE) images were created from characteristic areas of the thin sections, mineral phases were identified by their EDS spectra.

Sedimentological characteristics and facies interpretation of vertebrate sites in Villány Hills

The two studied vertebrate sites in the eastern part of Villány Hills expose the upper part of the Triassic succession.

- The *Construction site* is located on the Somssich Hill (45°52'28.9" N, 18°26'46.2" E; Fig. 1B), where productive and continuous excavations have been carried out in the last six years resulting in thousands of macro- and microvertebrate remains of fishes and reptiles in several beds of the Templomhegy Dolomite (Table 1), while the Mészhegy Formation was proved to be unfossiliferous.
- The *Road-cut section* on the Templom Hill (45°52'31.6" N, 18°26'55.5" E) exposes the Mészhegy Sandstone where a relatively diverse microvertebrate assemblage was discovered (Fig. 1B and Table 1).

The aim of the following subchapters is to present a detailed sedimentological description and interpretation of the Construction site. In this article, after discussing the interpreted depositional environment of this site, we provide an overview of the previous sedimentological works carried out on the siliciclastic succession of the Road-cut section and summarize the most recent interpretation of its depositional environment based on the newly discovered vertebrate microfossil material.

Construction site on the Somssich Hill

The Construction site is located southwest of the Villány railway station next to Arany János Street on the Somssich Hill (Fig. 1B). The exposed succession is about 20 meter long and 3–4 meter high, where around 17 meter thick succession of the upper part of the Templomhegy Dolomite and a very thin 3 meter thick sequence of the Mészhegy Sandstone crop out. The dominant formation of this site, the Templomhegy Member made up of southward-dipping (around 170/40 to 190/45) greyish dolomite and yellowish dolomarl beds with dolomitic claystone interlayers (Fig. 3). Here only the bone-bearing section of the Templomhegy Dolomite is discussed.

Sedimentological description and interpretation of the Construction site

Composition of the Templomhegy Member exposed in the Construction site is highly variable. It consists dominantly of dolomite, quartz and clay minerals, and subordinate amount of calcite (see Electronic supplement I). The grain size of siliciclastic components ranges from clay to sand size. Four lithofacies types were recognized, using a classification based on colour, grain size, bedding, fossil content and sedimentary structures (Figs. 3–9).

Dolomite lithofacies: This lithofacies is characterised by white to light pink dolomite beds (Fig. 4A–C). Mineralogically, this rock contains 80–96 % dolomite, while the clay minerals and quartz content is consistently low (<10 %). Although the carbonate rock is composed predominantly of dolomite,

the youngest, ~20 cm thick, layer of the succession (bed 29) contains 20 % calcite (Fig. 5). The feldspar content is very low throughout the investigated succession (<1 %). This lithofacies is common in the lowermost and the uppermost part of the site (Fig. 3), while the middle part of the section includes thinner dolomite layers occurring between dolomarl beds (Fig. 3D). The thickness of the beds decreases upwards in the section (30–40 cm in the lower and 10–15 cm in the upper part of the site).

The dolomite is usually aphanocrystalline and homogeneous in thin section (Fig. 6A), pointing to micritic precursor. Some beds show mottled fabric, where the crystal size is the same, but there are brownish patches, probably richer in micrometer-sized solid inclusions (Fig. 6B). The shape of such mottles is irregular. One sample is composed of aphanitic “sphaerules” of 200 to 300 micrometers, surrounded by very finely crystalline dolomite (Fig. 6C). The youngest dolomite layer of the exposed section (bed 29) contains a fine fracture system, along which the rock is calcitized/dedolomitized. The calcite contains few micrometer-sized remnants of dolomite and is intergrown with pyrite.

Vertebrate fossils are usually rare in this lithofacies, a few dozen bones and teeth of sauropterygians (Ősi et al. 2013) were discovered from it.

The dolomitic fabric suggests a lime mud precursor sediment. Samples with moderate fabric preservation suggest an originally ooidal carbonate sediment (Fig. 6C).

Therefore, this lithofacies can be interpreted as a carbonate mud deposited in a low-energy, shallow, restricted lagoonal environment (similar to Stockman et al. 1967; Brooks et al. 2003a,b; Blanchard et al. 2016), with episodic ooidal sediment transport. The probably reflux-related dolomitization of these sediments may have taken place in near surface setting.

Dolomarl lithofacies: A dominant lithofacies of this vertebrate site is yellowish to grey dolomarl with pale reddish coloured mottles (Fig. 4A,B and D). The thickness of such beds can vary from 10 cm to 50 cm. The clay content of the dolomarl beds varies considerably (Fig. 7).

Mineralogically, this lithofacies consists dominantly of dolomite (42–80 %), although the percentages of clay minerals may reach 30–20 % (Fig. 7). The dolomarl beds of the middle part of the section (beds 8–16) are characterized by a higher quartz content (20–30 %), while this mineral is subordinate (<5 %) in the other dolomarl horizons (see Electronic supplement I). The feldspar content is predominantly low and never exceeds 2 %. The more argillaceous dolomarl beds (e.g., bed 14) show a complex system of red clay-filled cracks (see below).

In thin section micrometer-sized dolomite crystals and clay particles are visible. Slight changes in crystal size and mottled fabric were commonly observed (Fig. 6D). There are brown pressure solution seams.

The vertebrate fossils are more common in those dolomarl beds which are characterized by lower carbonate and higher siliciclastic content. Bed 14 is particularly important in terms of chondrichtyan and osteichthyan fish remains; thousands of

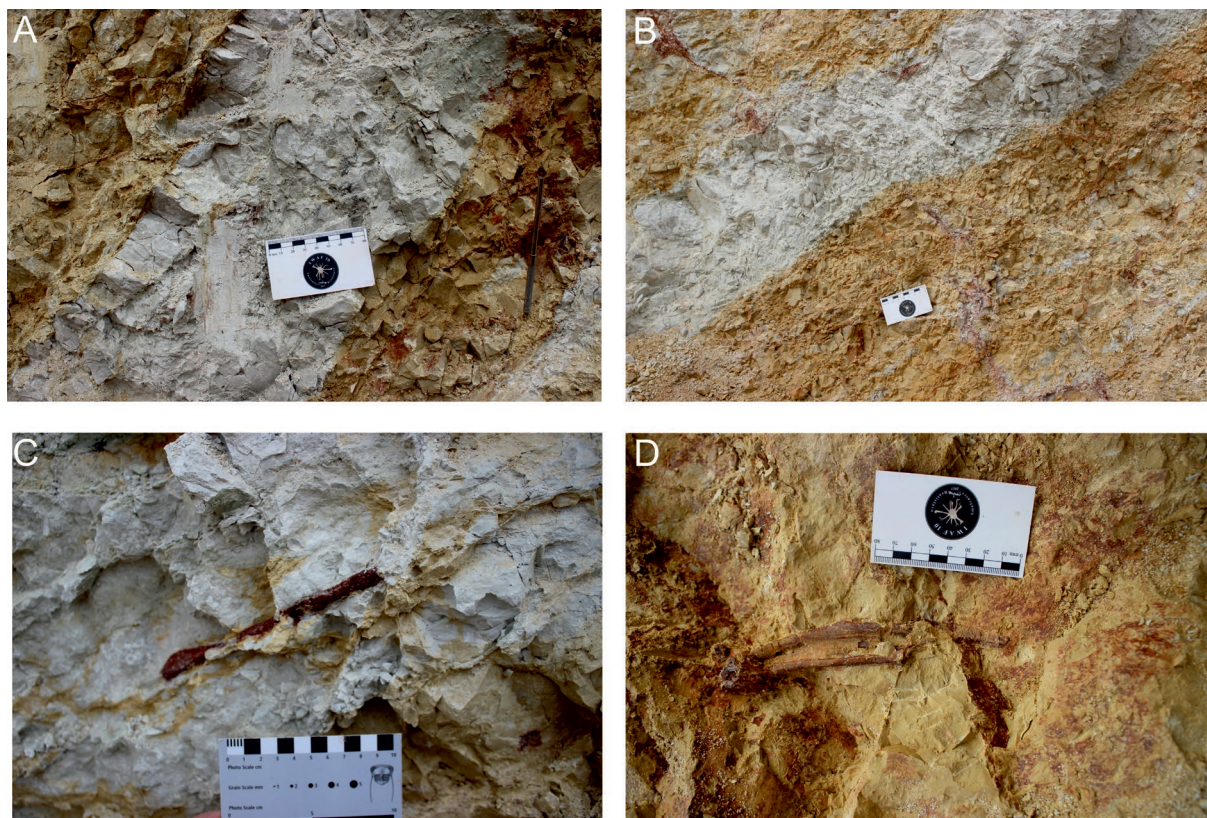


Fig. 4. The bone-bearing succession of the Construction site is made up by the alternation of yellowish grey dolomite and dolomarl layers (A, B). Dolomite (C) and dolomarl beds (D) with bones at the Construction site.

fish and sauropsid reptilian teeth and scales were collected from here (see Electronic supplement II). Bed 14 shows slightly different features than the other dolomarl layers at this site, because its top is pedogenetically modified (Fig. 8D–F and see below).

This lithofacies, comprising of mixed carbonate and fine siliciclastic (clay and silt) components, indicates a periodically changing terrigenous input, which was probably controlled by climatic and/or short-term sea-level changes (see below). The dolomitization, the lack of grainstone textures and the abundance of mud-dominated lithologies, as well as the presence of pedogenetically modified dolomarl beds (see below) suggest that this facies was formed in a low energy, restricted shallow marine environment. The pale reddish stain in the argillaceous marl sediments probably indicates a more intense oxidation due to the influence of meteoric water during periodic subaerial exposure.

Reddish silty claystone: The reddish silty claystone with pale yellow mottles represents the third lithofacies in the observed section (Fig. 8). There are three claystone horizons (top of bed 14, beds 21 and 27) in the section; their thickness does not exceed 10 cm (Fig. 3A). These rocks are characterized by a higher quartz (~20 %) and a lower dolomite content (~20 %) than that of the dolomarl lithofacies (see Electronic supplement I). Dispersed pale yellow mottles are relatively common in this facies. Tiny cylindrical, poorly

preserved vertical root casts and weakly defined nodules can also be detected (Fig. 8). Yellowish carbonate and reddish brown clay rich patches show a mottled appearance in thin section (Fig. 6E). Red colour of the clay rich part is due to fine-crystalline hematite. Two slightly different types of this lithofacies can be distinguished:

- Dark red, slightly calcareous, homogenous layer with tiny irregular yellowish root traces. It usually forms a distinct layer between two dolomarl beds (bed 21). No vertebrate fossils has been found in it (Fig. 8A,B);
- Silty claystone of higher dolomite content, rich in carbonate nodules. It is developing through a continuous transition from the underlying dolomarl beds (top of bed 14). Fragmented carbonate crusts showing poorly definable tepee structure and laminated micritic horizons are present in the uppermost part of this thin claystone layer (Fig. 8D–F).

The reddish colour and the vertical root casts indicate that this claystone was better drained than the other argillaceous carbonates in the section. Based on its mineral content (dominated by non-carbonate minerals), macrofeatures (root moulds, fine-grained layers with Liesegang-bands and mottles) and colour, this horizon is interpreted as calcic paleosol (similar to Klappa 1980a,b; Wright 1994; Kraus 1999). The red colour implies the abundance of ferric oxides indicating oxidizing conditions and well-drained environment during pedogenesis (Wright 1994; Kraus 1999; Zand-Moghadam et al. 2014;

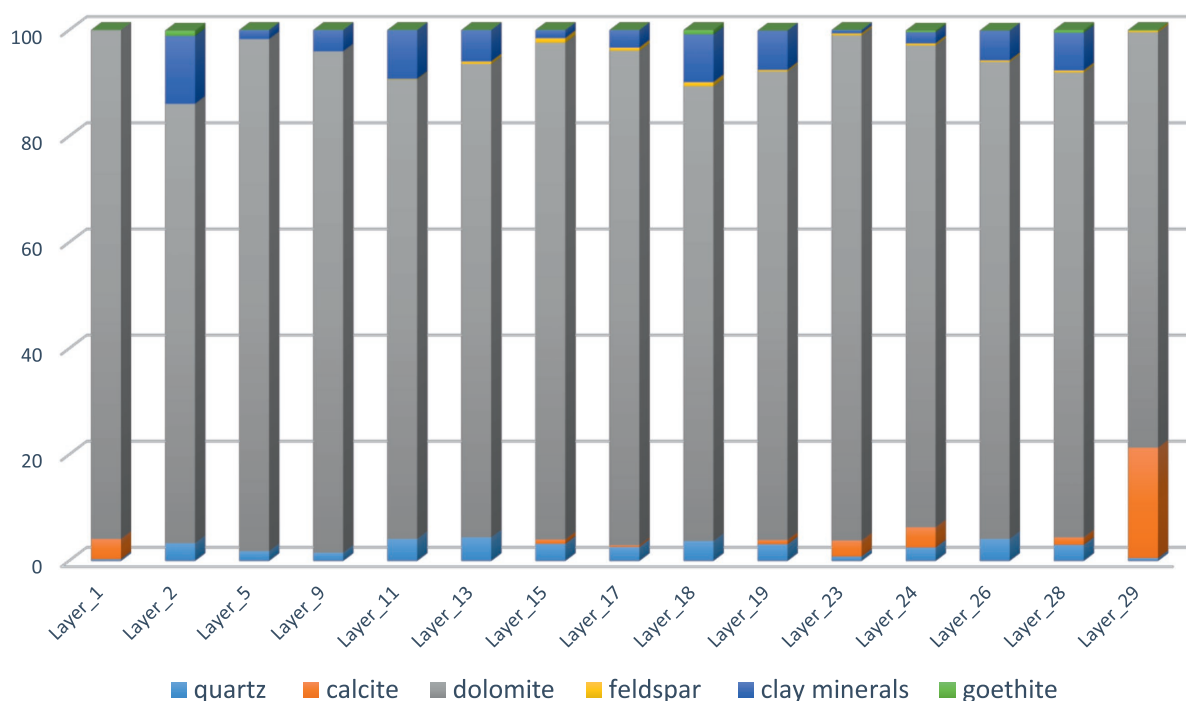


Fig. 5. Mineralogical composition of dolomite beds of the Construction site, based on XRD analyses (see Electronic supplement I). The layer numbers are shown in Fig. 3A.

Huggett et al. 2016). The laminated claystone horizons in the uppermost part of bed 14 can be interpreted as dolocretes (Fig. 8F) and may have been formed by microbial mediation (similar to Wright 1994: fig.4). The presence of tepee structure (Fig. 8E), dolocretes, as well as the vertical root moulds indicate that these silty claystone sediments have been subaerially exposed, during which they were modified by pedogenetic processes. The peritidal environment is regularly exposed to subaerial conditions during low sea-level stages resulting in the development of thin paleosol horizons on top of the carbonate sediments (Ginsburg 1975; Wright 1994; Blanchard et al. 2016; Huggett et al. 2016).

Sandy claystone: This is a single greenish, greyish, 80 to 100 cm thick, moderately to weakly calcareous sandy claystone bed (bed 10) with subordinate clay intercalations (Figs. 3A and 9). Quartz is the most abundant component (about 50 %), while the clay mineral content shows an upward increasing trend reaching about 50 % at the top of the layer. The rock is characterized by a relatively high feldspar content (about 12 %), but this quantity suddenly decreases in the upper part of the layer, where the clay content increases (Fig. 9B).

The microscopic texture is characterized by a very fine-grained clay-rich matrix in which coarser grained, quartz-rich, sometimes lenticular domains occur (Fig. 9C,D).

Based on the SEM analysis, the fine grained component consists of illite (90–95 %), quartz (3–5 %), K-feldspar (<1 %), calcite (1–2 %) and accessory minerals: glauconite, biotite, magnetite, zircon (<1 % respectively). Quartz grains are mostly 5–10 µm in size, biggest ones can reach 25–30 µm. K-feldspar is usually much smaller, maximal grain size is

~15–20 µm. The laminae of the claystone is densely penetrated by slightly undulating cracks, which are more or less parallel with the longer axes of the quartz rich lenses. The transition towards the coarser grained domains and towards the adjacent carbonate layers is continuous.

Based on the SEM and polarising microscopy analysis, the fine-grained sandstone lenses consist mostly of subangular to very angular, xenomorphic quartz (60–90 %) and K-feldspar grains (5–10 %); kaolinite (5–10 %) and accessory minerals: Ti-magnetite, muscovite, rutile, zircon, calcite and rock fragments (<1 % respectively). The size distribution of the quartz grains is bimodal with two peaks at ~50 and 200–250 µm. Undulatory extinction of quartz is common. Amongst the quartz crystals with normal extinction there are rounded grains — similar to resorbed volcanic crystals. Feldspar grains have an average size of 150–200 µm, and they are often strongly fractured.

The rock forming minerals suggest a terrigenous provenance. The significant amount of quartz crystals with undulatory extinction, the lack of plagioclase, amphibole or pyroxene crystals and even altered volcanic glass fragments exclude the pyroclastic origin. Although there are some minerals — biotite, zircon, glauconite and presumably resorbed quartz grains — which could be derived from resedimented pyroclastics/volcanoclastics. The dominance of angular to subangular grains and the significant amount of K-feldspar in the sand fraction denote a short transportation path and a nearby source area. The textural features suggest that the clay minerals are probably allogenic (illite) in the matrix and most likely authigenic (kaolinite) in the lenticular sandstone domains.

Road-cut site on the Templom Hill

The Road-cut section, exposed on the Templom Hill in Villány (Fig. 1B), was excavated and cleaned up many times over the last century. In the first short sedimentological description, given by Rálich-Felgenhauer (1985), the succession was interpreted as being shallow marine or littoral. Later Vörös (2009) suggested that the siliciclastic sediments of the Road-cut section represent three phases of fluviolacustrine deposition in a local, Late Triassic basin. In 2012 the section was cleaned up in order to determine the source area of the sediment based on petrographical analyses. Pozsgai et al.

(2017) indicate adjacent source area, composed of mainly Ordovician medium-grade metamorphic rocks, for the siliciclastic succession. Currently the Road-cut section is in a very poor state due to the lush vegetation and the less resistant sediment types. However, thanks to the detailed geological research, conducted over the past decades (Rálich-Felgenhauer 1985; Vörös 2010; Ősi et al. 2013), the Road-cut section is well documented. Therefore we only briefly summarize the sedimentological descriptions and provide some new observations and paleontological data, which may contribute to better understanding the conditions of the depositional environment of this sediment accumulation.

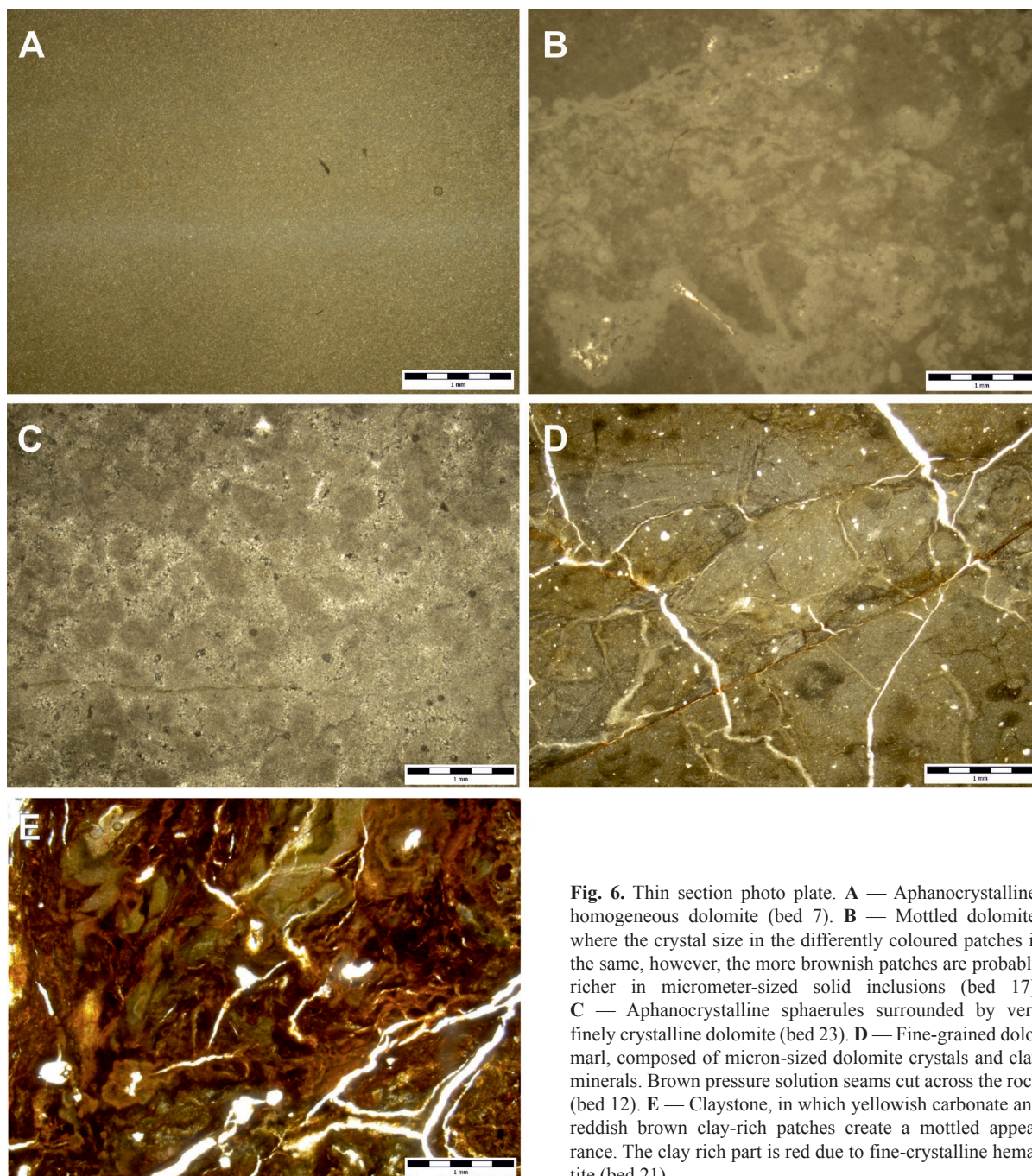


Fig. 6. Thin section photo plate. **A** — Aphanocrystalline, homogeneous dolomite (bed 7). **B** — Mottled dolomite, where the crystal size in the differently coloured patches is the same, however, the more brownish patches are probably richer in micrometer-sized solid inclusions (bed 17). **C** — Aphanocrystalline sphaerules surrounded by very finely crystalline dolomite (bed 23). **D** — Fine-grained dolomarl, composed of micron-sized dolomite crystals and clay minerals. Brown pressure solution seams cut across the rock (bed 12). **E** — Claystone, in which yellowish carbonate and reddish brown clay-rich patches create a mottled appearance. The clay rich part is red due to fine-crystalline hematite (bed 21).

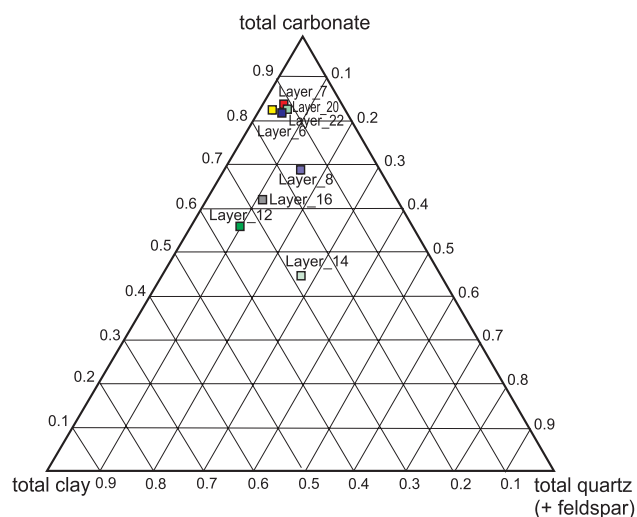


Fig. 7. Ternary diagram of dolomarl and claystone beds of the construction site based on the results of XRD analyses. The layer numbers are shown in the Fig. 3A.

Sedimentological description of the Road-cut site

The Road-cut site („Siklóbevágás” in Hungarian) is nearly 30 meter-long and 3–5 meter-high, where three formations are exposed (Fig. 10).

The uppermost beds of the Templomhegy Member is exposed in the northern part of the Road-cut site. The dolomite and yellowish dolomarl beds are similar to the uppermost exposed dolomite beds of the Construction site (Pozsgai et al. 2017). This part of the sequence is dominated by whitish dolomite and yellowish dolomarl beds, frequently intercalated by very thin (few-mm-thick) reddish, yellowish or greenish claystones.

Only one exception is a 15-cm-thick, variegated claystone layer that is dominantly reddish and greenish, yellowish, purplish mottled, and contains lenticular, indurated, calcareous intercalations. This bed contains elongated carbonate concretions and angular dolomite clasts as well. On the top of the claystone bed, a friable carbonate crust occurs. This clayey intercalation is probably identical to the reddish claystone with calcareous crust in the Construction site (see Fig. 8). The water-screened residue of Templomhegy Member at the Road-cut site was not productive for fish fossils, but a few poorly preserved sauropterygian bones were discovered from these horizons (Ősi et al. 2013).

The siliciclastic content of the rocks increases upwards in the section and the Templomhegy Member is overlain by an almost 15-m-thick sequence of the Mészhegy Sandstone Formation (Vörös 2009; Fig. 10B), which is made up of cyclic alternation of weakly cemented, greyish, yellowish, purplish or greenish sandstone and siltstone layers, reddish, purplish or variegated clay strata, and subordinately greyish dolomite and yellowish dolomarl beds (Vörös 2010; Pozsgai et al. 2017). Although several sharp surfaces dissect the succession (Vörös 2009), no unequivocal boundary can be recognised between

the Templomhegy Dolomite and the Mészhegy Sandstone in this section. However, in agreement with Vörös (2010), we also suggest to define the boundary between the two formations at the level where a continuous sandstone–siltstone–claystone assemblage overlies the carbonate dominated strata in the section.

The sediments of Mészhegy Sandstone Formation in the Road-cut section can be divided into the following major lithofacies (based on Rálich-Felgenhauer 1985; Vörös 2009, 2010; Pozsgai et al. 2017; Fig. 11):

Conglomerate (Fig. 11A): Only one conglomerate bed occurs in the section. It is 50-cm-thick and unconformably overlies a claystone horizon. It is a matrix supported (with a carbonatic, clayey, sandy matrix), polymict conglomerate includes upward fining, rounded clasts (dolomite, dolomarl, limestone, sandstone, claystone and polycrystalline quartz clasts).

Sandstone (Fig. 11B): These are fine to coarse grained, (sublitharenite, subarcose) sandstones. In the lower part of the section mainly greyish sandstones are present, containing reworked rounded claystone (1–2 cm) and angular marl clasts (1–10 cm) and smaller amount of quartz pebbles (<0.5 cm). In the upper part of the section greenish, reddish, purplish, greyish sandstones layers occur. Crossbedding is locally visible.

Claystone, silty and sandy claystone (Fig. 11C,D): This is the dominant lithofacies in the Road-cut section. The claystone frequently include greyish, fine-grained, lenticular sandstone bodies. Greenish siltstone and variegated claystone beds appear in the older part of the section whereas yellowish, brownish claystone and claystone layers occur in the upper part.

Cellular marl (Fig. 11E,F): Yellowish marl beds, which are characterized by polygonal cracks and cellular structure. Its mineralogical composition is dominated by calcite (around 75 %); illite (10 %), kaolinite (10 %) and quartz (5 %) also occur. Calcite veins (0.5–2 cm thick) are very common.

Several beds of the Mészhegy Sandstone Formation were sampled for screen-washing, but only three brownish-greyish sandstone beds (L3–L4–L5) yielded microvertebrate remains (Fig. 10 and see Electronic supplement II). The most abundant vertebrate material was recovered from the uppermost sandstone bed (L5 in Fig. 10B), which provided more than three hundred teeth and scales from different marine fish and sauropsid reptilian taxa (see Table 1). The Triassic sequence of the Road-cut site on Templom Hill is covered by the Pliensbachian Somssichhegy Limestone Formation (Fig. 10).

Discussion

The succession of the Construction site is composed predominantly of carbonates (dolomite) with various clay content, i.e. it is made up of alternating dolomite and dolomarl layers (Fig. 3). At the outcrop scale, we use the terms “dolomarl” and “dolomite” in a descriptive sense, the more massive and solid, light-coloured beds with high dolomite content

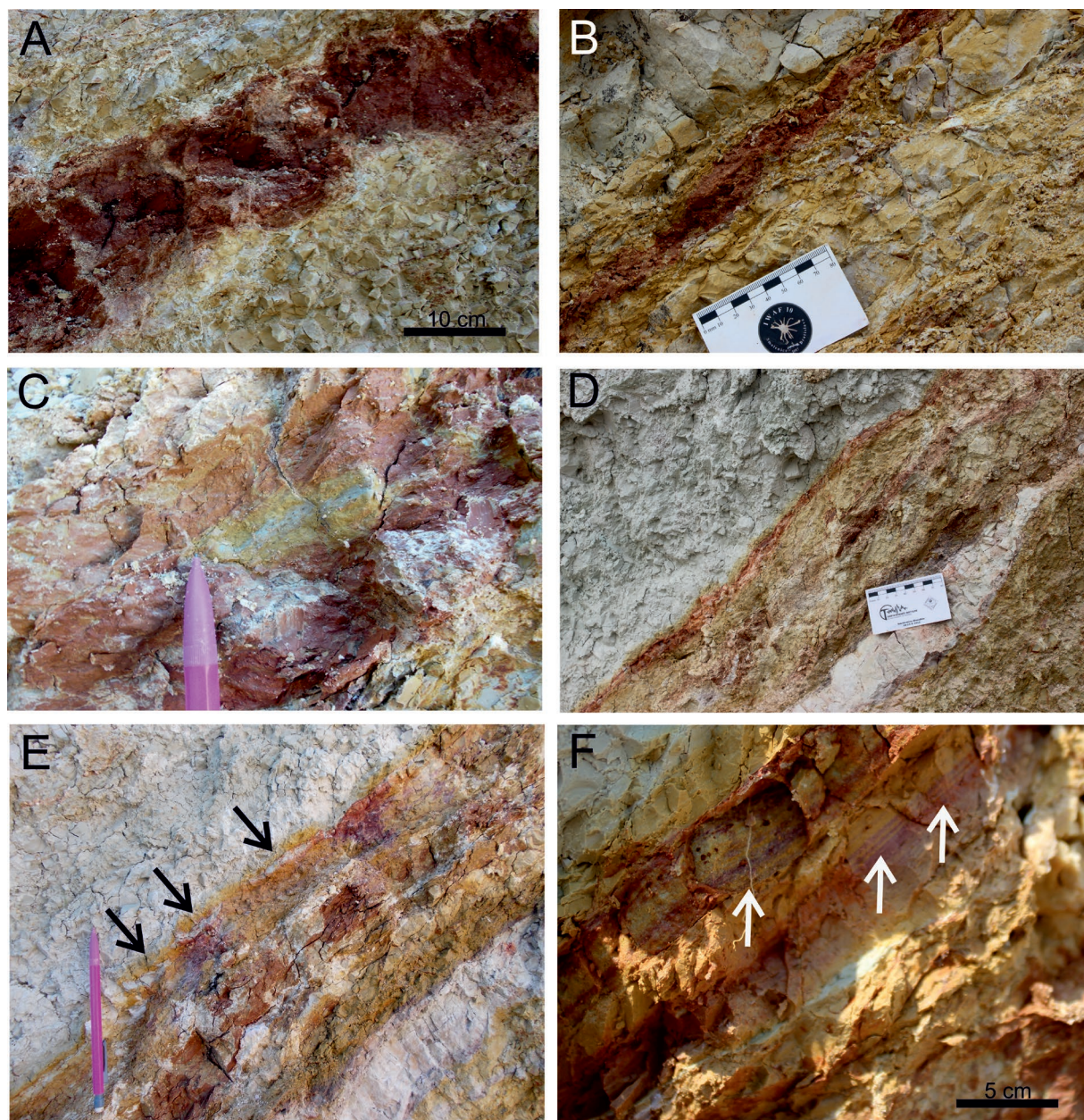


Fig. 8. Reddish silty claystone layers at the Construction site. Dark red, slightly calcareous, homogenous unfossiliferous claystone bed (A, B). Pale yellow mottle in the reddish claystone body (C). The most important fossiliferous horizon (bed 14) of the Construction site (D). Fragmented carbonate crusts, showing poorly definable tepee structure (E), and laminated micritic horizons (F) are present in the uppermost part of the bed 14.

(80–95 %) are classified as argillaceous dolomites beds, while the softer and colourful layers, characterized by lower dolomite content (<80 %) are classified as dolomarl interlayers (Fig. 4).

Due to the facies analyses of the Construction site four main lithofacies were identified. They were formed in the inner ramp lagoon and related tidal flat environments. The carbonate sediments of the dolomite lithofacies were deposited in a shallow, restricted lagoon environment, dolomarl (shallow marine sediments, where the enhanced terrigenous input was the results of the more humid climate), reddish silty claystone

(paleosol) and sandstone (terrigenous provenance) indicating that the sediments of the Construction site were formed in inner ramp lagoon and related tidal flat environments. The alternation of siliciclast rich and carbonate rich sediments can be frequently interpreted as the results of short-term sea-level or climate changes (e.g., Wilson 1967; Brachert et al. 2003; Colombié et al. 2012; Caracciolo et al. 2013; Zeller et al. 2015; Blanchard et al. 2016; Reis & Suss 2016; Chiarella et al. 2017). The short-term sea-level changes have a significant control on the sedimentation of the shallow marine environment, because during the lowstands, carbonate sediment

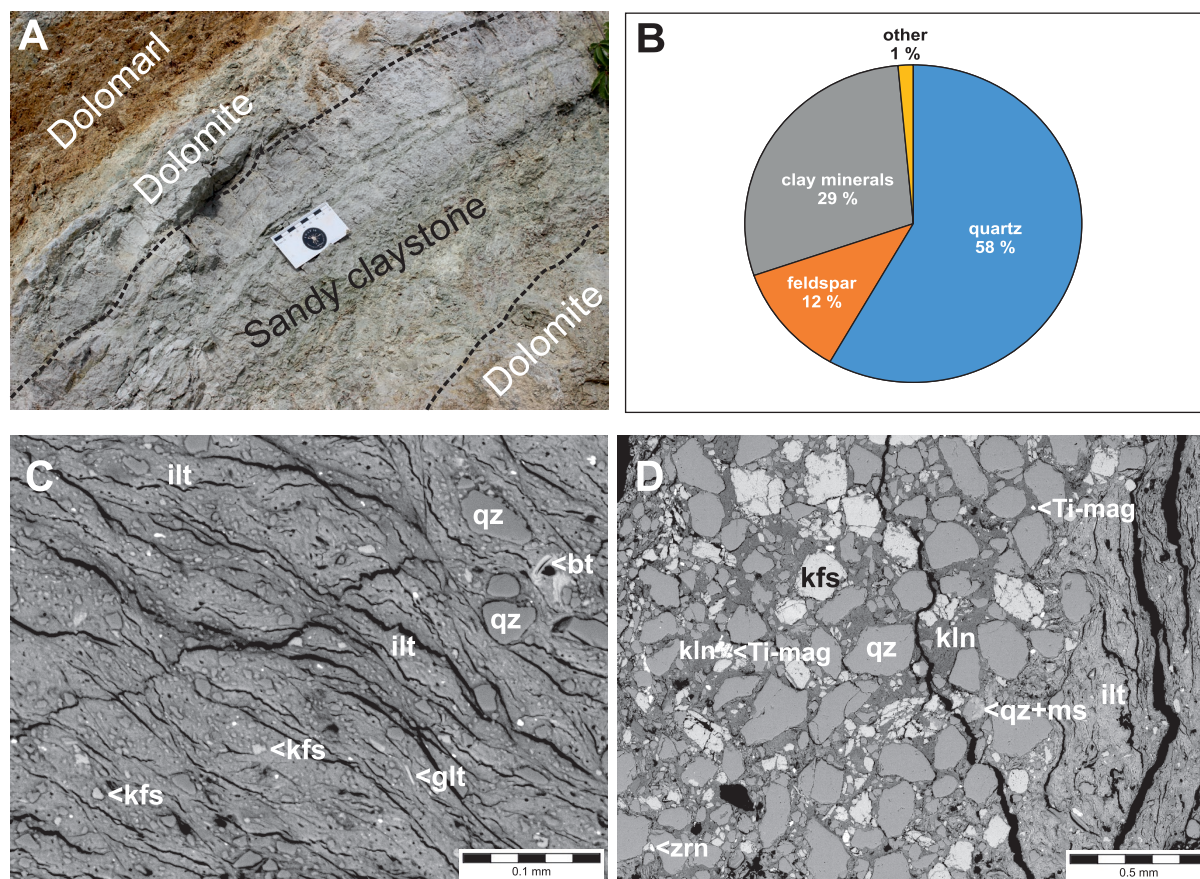


Fig. 9. **A** — Sandy claystone bed of the construction site and its mineral composition (**B**) based on XRD analyses (see Electronic supplement I). **C** — Claystone composed of illite, quartz, K-feldspar, calcite and accessory minerals: glauconite, biotite, magnetite, and zircon. Backscattered electron image (bed 10). **D** — Fine-grained sandstone, consisting of subangular to angular, xenomorphic quartz and K-feldspar crystals; kaolinite and accessory minerals: Ti-magnetite, muscovite, rutile, zircon, calcite and rock fragments. The transition towards the finer grained domains is continuous. Backscattered electron image (bed 10).

production is slowed down or halted and the terrigenous influx can increase, resulting in the predominance of siliciclast deposition (Wilson 1967; Brachert et al. 2003; Carcel et al. 2010; Caracciolo et al. 2013; Chiarella et al. 2017 and references therein). The short-term climate changes play also an important role in marine areas near the mainland (Coffey & Read 2007; Caracciolo et al. 2013; Zeller et al. 2015). The humidity significantly influences the terrigenous sediment influx from the land to the marine realm and thus the carbonates formed during the dryer periods are frequently replaced by siliciclastic sediments during humid conditions.

The observed succession was deposited near to the land in an inner ramp lagoon and the related tidal flat environments where the siliciclastic input and coeval carbonate production were significantly controlled by different allocyclic (e.g., climatic or sea-level changes) factors (see also Brachert et al. 2003; Colombié et al. 2012; Chiarella et al. 2017). The studied section of the Construction site was deposited between the Late Anisian and Carnian based on its stratigraphic position (Rálsch-Felgenhauer & Török 1993; Török 1998; Haas 2001) and vertebrate fossils (Ősi et al. 2013), which period was frequently characterized by significant fluctuation in

the climatic conditions and rainfall intensity (e.g., Mutti & Weissert 1995; Simms et al. 1995; Feist-Burkhardt et al. 2008; Preto et al. 2010). We suggest that the interval of higher siliciclast content observed in the middle part of the section (beds 10 to 22; Fig. 3), between two carbonate rich sequences, reflects a temporary change in the prevailing climate (Fig. 12). The lower and upper part of the studied section was formed in the periods of more arid climate, when the siliciclastic influx from the land was subordinate, while the middle part of the section that is characterized by higher siliciclastic content (including sandstone and claystone beds) was deposited during a more humid phase of enhanced rainfall intensity. Furthermore, the reddish silty claystone facies (Fig. 8) situated in the middle part of the section, represents recurring paleosol formation, and indicates that the marine sediments were repeatedly exposed to subaerial conditions, suggesting relative sea-level falls (Fig. 12). A global sea-level fall was recognized around the Late Ladinian and Early Carnian by Haq et al. (1988) and Ruffell (1991), which period coincides with the assumed depositional age of the carbonate-dominated sedimentary sequence of the Construction site and thus this eustatic change might be correlated with

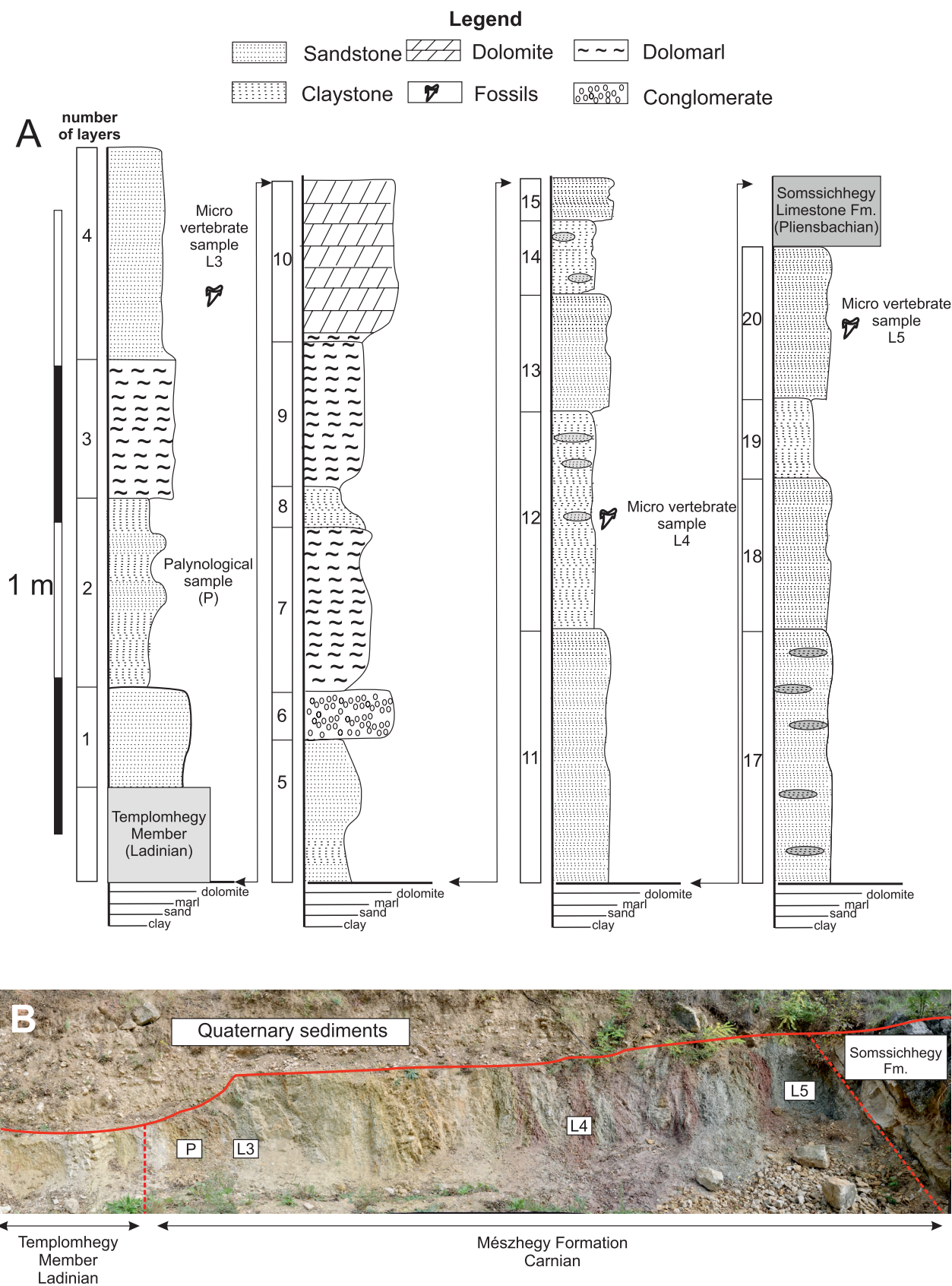


Fig. 10. Schematic stratigraphic section of the Road-cut section (A) and picture of the Carnian fossiliferous horizons of the Mészhegy Sandstone Formation with marks of the beds which providing paleontological data (B). P=palynological sample, L3–L5=vertebrate paleontological samples (after Ősi et al. 2013).

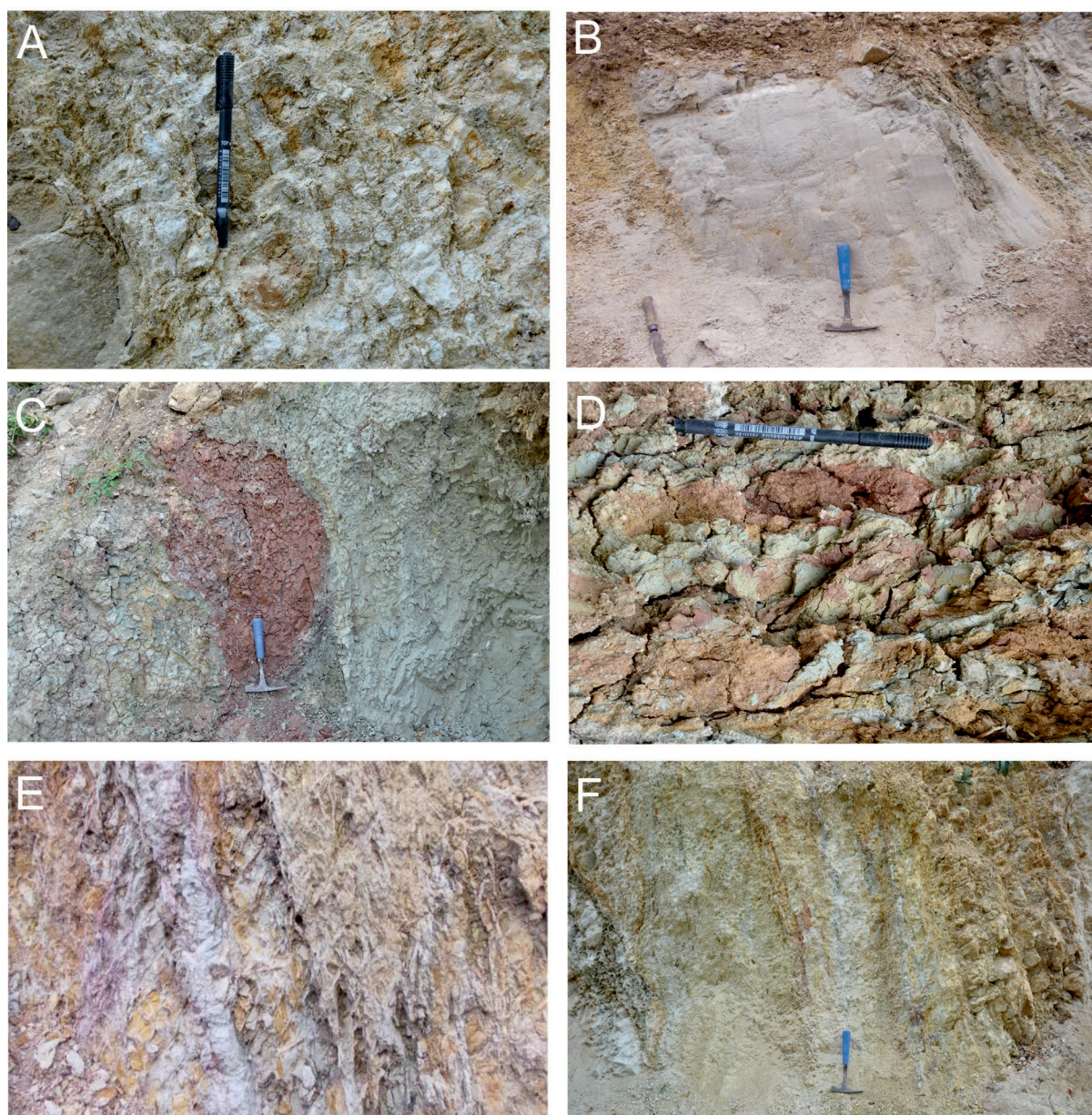


Fig. 11. The main sediment types of the Mészhegy Sandstone Formation in the Road-cut section. Polymict conglomerate (A), fine to coarse grained sandstone (B), red claystone between greenish sandy claystone (left) and greenish sandstone (right) bodies (C), variegated claystone (D), cellular dolomitic limestone (E, F).

the presence of paleosol horizons in the middle part of this section.

The middle part of the Construction site is extremely important from a paleontological point of view, because it includes the most productive bone-bearing layers from where thousands of vertebrate fossils were discovered (Ősi et al. 2013). Though vertebrate fossils can be found essentially all over the middle part of the section, the bone and teeth accumulation is most significant in those layers that are characterized by a higher clay content (e.g., beds 14–16; Fig. 7). Fishes are abundant microfossils, classified to both chondrichthyan (e.g., *Palaeobates*) and osteichthyan (e.g., *Gyrolepis*) taxa,

indicating typical marine conditions during the bonebed deposition (see Electronic supplement II). The Templomhegy Dolomite yielded a fish fauna dominated by durophagous hybodontiforms (*Palaeobates* and *Lissodus*; altogether 1302 tooth remains, meaning 71.9 % of total), which is significantly different from that discovered in the overlying Mészhegy Sandstone Formation (see in Electronic supplement II, and see below).

Based on the sedimentological investigation, the changes in the depositional environment through the sediment accumulation at the Construction site can be summarized as follows (see Fig. 12). The lower part of the observed section (beds 1–9;

Fig. 3) is made up of dominantly aphanitic to very finely crystalline dolomite beds with subordinate argillaceous deposits. This part of the section can be characterized by carbonate sedimentation where the siliciclastic influx from the land was subordinate. This part of the section was deposited in the inner ramp zone was flooded due to sea-level rise. The top of this interval corresponds to a relatively thick sandstone bed (bed 10; see Figs. 3 and 9A), located between the massive dolomite and the most marly interval. This sandstone with high quartz content indicates that the climate has become more humid and significant siliciclastic influx arrived from the land (Fig. 9B). Above this layer, more argillaceous sediment (dolomarl beds) can be observed representing the middle part of the section (beds 10 to 22; Fig. 3). This part was most likely deposited in a period, when the fine terrigenous input significantly increased most probably due to the enhanced humidity allowing the accumulation of more argillaceous sediments. The increase in clastic influx may have been also related to a relative sea-level fall, because the presence of reddish silty claystone bed in this part of the section shows evidence of subaerial exposure. The pedogenesis took place under oxidizing conditions, as indicated by the red colour of the claystone bed (Construction site; top of beds 14 and 21). However, neither karstic features nor downcutting by streams were observed, indicating that the subaerial exposure was relatively short (e.g. Wilson 1967). The middle part of the section is covered by beds of massive, homogenous very finely crystalline dolomite (beds 23–29; Fig. 3) with thin dolomarl intercalations, where the vertebrate fossils are very rare. Dolomarl beds in this section are characterized by a high dolomite content (about 85 %) indicating that the carbonate sedimentation became dominant again while the amount of siliciclastic sediments decreased. The low siliciclastic content and the lack of traces of pedogenesis in the youngest part of Templomhegy Member exposed in Construction site suggest a more arid condition and a sea-level rise during the accumulation.

The last dolomitic layer is unconformably covered by a thinner siliciclastic sediment package which is composed of sandstone, siltstone and claystone beds. The vertebrate fossils are completely absent from this sequence, but the petrographical analyses indicates that this clastic succession is part of the Carnian Mészhegy Sandstone Formation (Pozsgai et al. 2017). The sediments of the Mészhegy Sandstone Formation can be better investigated at the Road-cut site where its 15-meter thick sequence is exposed (Rálich-Felgenhauer 1985; Vörös 2009, 2010).

Despite the several decades of research in the Road-cut section, the age and the depositional environment was difficult to define, because the mentioned authors did not find any fossils which they could use for more detailed paleoenvironmental reconstruction. The unfossiliferous nature of this formation (except for some unidentified reptile bones) remained an accepted viewpoint until the discovery of a relatively rich vertebrate assemblage in 2012. The discovered fish remains (e.g., *Paleobates angustissimus*, *Gyrolepis* sp.) indicates a marine environment for at least the sampled beds, that are

situated in the lower (bed L3; Fig. 10B) and the upper part (beds L4–L5; Fig. 10B) of the Road-cut section (Fig. 10 and Electronic supplement II). The fish fauna of the Mészhegy Sandstone Formation (dominated by *Hybodus*) is significantly different from that of the Templomhegy Dolomite Member (dominated by durophagous hybodontiforms, such as *Paleobates* and *Lissodus*). Therefore the fish fossils of the Road-cut site cannot be derived from the underlying marine deposits (for detailed differences in the fauna compositions see Electronic supplement II). Furthermore, besides collecting vertebrate fossils, several samples were also taken for palynological investigations. One of these (from a sandy-claystone bed from the lowermost part of the section; see Fig. 10B) has provided a relatively diverse sporomorph assemblage (*Patinasporites densus*, *Infernopollentites* sp., *Aratrisporites* spp., *Ovalipollis* spp., and *Triadispora* spp.) indicating a Carnian age for the lower part of the section (Ősi et al. 2013). This also suggests that the sediments were deposited in a nearshore environment characterized by a high input of land-derived organic matter (Ősi et al. 2013). Nevertheless, the collected fossils are not sufficient to completely exclude the possibility of fluviolacustrine sedimentation in the succession exposed in the Road-cut section (see Vörös 2009, 2010). However, we suggest that at least four fossil-bearing sandstone beds, occurring in the lowermost and the uppermost part of the section, were deposited in a nearshore (based on palynological data; Ősi et al. 2013), shallow marine environment (based on marine fish assemblage) characterized by intense terrigenous input.

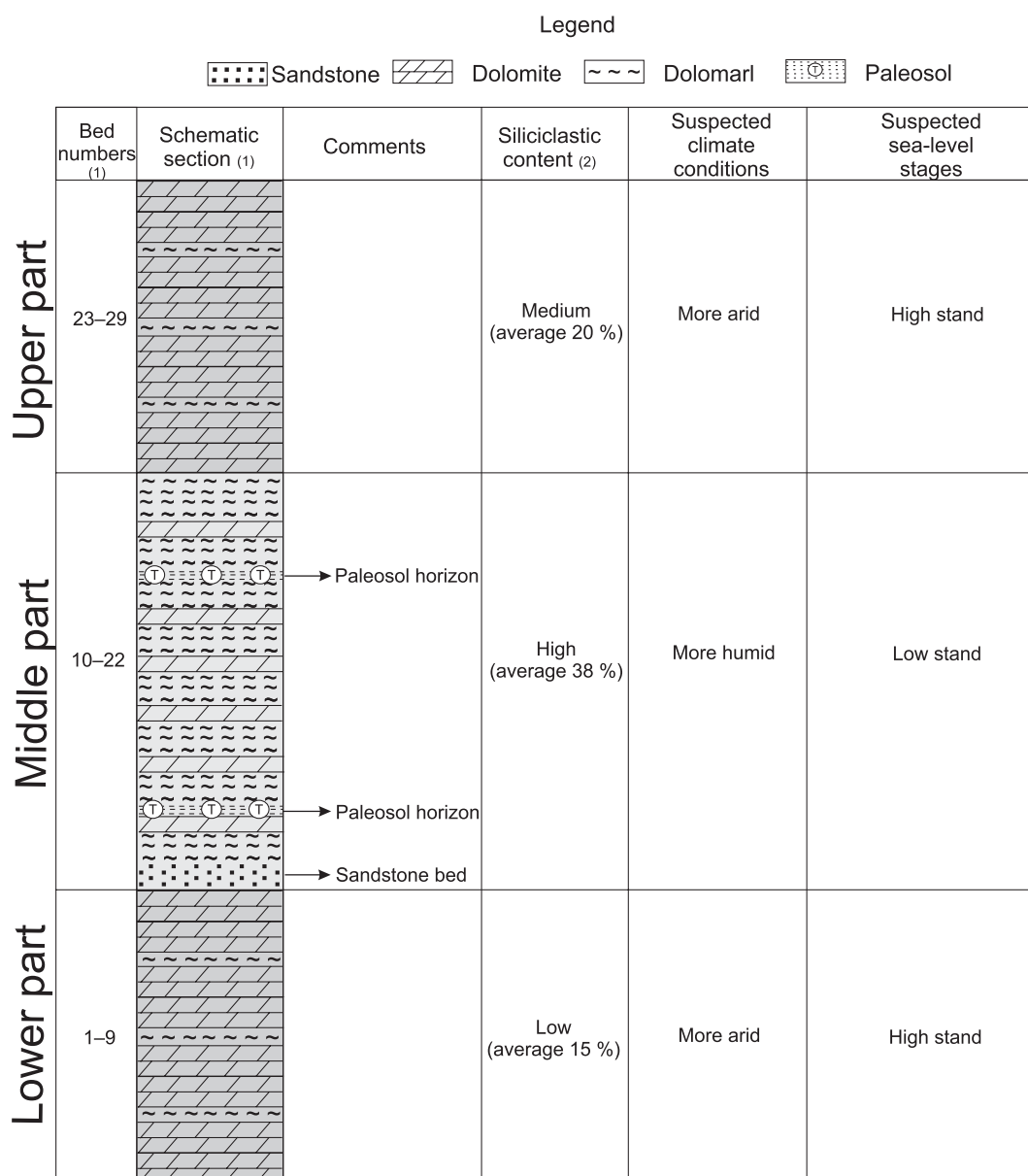
Conclusions

1. Four main lithofacies were identified and interpreted in the newly discovered Construction vertebrate site, which is dominantly made up of alternating dolomite and dolomarl layers. The four lithofacies units can be defined as follows:
 - dolomite, deposited in a shallow, restricted lagoon environment;
 - dolomarl, as shallow marine sediment, where the enhanced terrigenous input was the results of the more humid climate;
 - reddish silty claystone, formed as paleosol;
 - sandstone indicating a terrigenous input.
2. The stratigraphical, sedimentological and paleontological investigations revealed that the sediments of the Construction vertebrate site were formed in the nearshore (subtidal to peritidal) zone of a ramp, where the alternating sedimentation was mostly controlled by climatic changes. However, the recurring paleosol formation in the middle part of the section also indicates episodic sea-level fall events, when the marine sediments were repeatedly exposed to subaerial conditions.
3. The Construction site can be divided into three main parts: the lower part (from bed 1 to 9) can be characterized by carbonate sedimentation where the siliciclastic influx from

the land was subordinate. The top of this interval corresponds to a relatively thick sandstone bed with high quartz content indicating that the climate became more humid, and significant siliciclastic influx arrived from the land. Above this horizon, the middle part of the section (from bed 11 to 22, including the richest bone-bearing horizons) was most probably deposited in the period, when the siliciclastic input from the land remained significant and the paleosol horizons may have been related to relative sea-level fall. The upper part (from bed 23 to 29) is composed of homogenous micritic dolomite succession with subordinate thin dolomarl intercalations, indicating that the carbonate sedimentation

became dominant again while the amount of siliciclastic sediments significantly decreased.

4. The bone-bearing horizons of the Construction site were encountered in the middle part of the section (beds 11 to 22). The most significant bone and teeth accumulation occur in these layers (beds 14–16) which are characterized by a higher siliciclast content.
5. Sedimentological and paleontological investigations of the Road-cut section suggest that the main part of this succession (at least four fossil-bearing layers occurring in the lowermost and the uppermost part of the siliciclastic sequence) were deposited in a nearshore, shallow marine



(1) see Fig. 3

(2) see Electronic supplement I.

Fig. 12. Simplified section of the Construction site showing the suspected changes in the prevailing climate and sea-level during its deposition.

environment characterized by high siliciclastic input from the mainland.

Acknowledgments: We thank Annette E. Götz, János Haas and Attila Vörös for their useful comments and suggestions that greatly improved our manuscript. The authors are eminently thankful to Gyula Konrád, Krisztina Sebe, Tamás Budai, István Dunkl, Emese Szöcs, Andrea Mindszenty, Georgina Lukoczki, Orsolya Sztanó, György Czuppon and Sándor Józsa for useful discussions and consultations. The authors are grateful to Krisztina Buczkó and Kristóf Fehér for their help in performing scanning electron microscopy micrographs. We thank Réka Kalmár and János Magyar for technical assistance. Our work was supported by the National Research, Development and Innovation Office (NKFIH K116665 and K124313), Hungarian Academy of Sciences Lendület Program, Hungarian Natural History Museum, Eötvös Loránd University, University of Pécs, University of Göttingen, and the Danube–Dráva National Park.

References

- Bérczi-Makk A., Konrád Gy., Rálich-Felgenhauer E. & Török Á. 2004: Tisza Mega-unit. In: Haas J. (Ed.): *Geology of Hungary, Triassic*. ELTE Eötvös Press, Budapest, 303–360 (in Hungarian).
- Blanchard S., Fielding C. R., Frank T. D. & Barrick, J. E. 2016: Sequence stratigraphic framework for mixed aeolian, peritidal and marine environments: Insights from the Pennsylvanian subtropical record of Western Pangaea. *Sedimentology* 63, 7, 1929–1970.
- Bleahu M., Bordea S., Panin Ș., Ștefănescu, M., Šikić K., Haas J., Kovács S., Péro, Cs., Bérczi-Makk A., Konrád Gy., Nagy E., Rálich-Felgenhauer E. & Török Á. 1994: Triassic facies types, evolution and paleogeographic relations of the Tisza Megaunit. *Acta Geologica Hungarica* 37, 3–4, 187–234.
- Böttcher R. 2015: 8. Fische des Lettenkeupers. In: Hagdorn H., Schoch R. & Schweigert G. (Eds.): *Der Lettenkeuper — Ein Fenster in die Zeit vor den Dinosauriern*. *Palaeodiversity*, Sonderband, 141–202.
- Brachert T.C., Forst M.H., Pais J.J., Legoinha P. & Reijmer J.J.G. 2003: Lowstand carbonates, highstand sandstones? *Sediment. Geol.* 155, 1–2, 1–12.
- Brooks G.R., Doyle L.J., Suthard B.C., Locker S.D. & Hine A.C. 2003a: Facies architecture of the mixed carbonate/siliciclastic inner continental shelf of west-central Florida: implications for Holocene barrier development. *Mar. Geol.* 200, 1–4, 325–349.
- Brooks G.R., Doyle L.J., Davis R.A., DeWitt N.T. & Suthard B.C. 2003b: Patterns and controls of surface sediment distribution: west-central Florida inner shelf. *Mar. Geol.* 200, 1–4, 307–324.
- Burchette T.P. & Wright V.P. 1992: Carbonate ramp depositional systems. *Sediment. Geol.* 79, 1–4, 3–57.
- Cappetta H. 2012: Handbook of Paleoichthyology, Vol. 3E: Chondrichthyes. Mesozoic and Cenozoic Elasmobranchii: Teeth. *Verlag Dr. Friedrich Pfeil*. 1–512.
- Caracciolo L., Gramigna P., Critelli S., Calzona A.B. & Russo F. 2013: Petrostratigraphic analysis of a Late Miocene mixed siliciclastic–carbonate depositional system (Calabria, Southern Italy): implications for mediterranean paleogeography. *Sediment. Geol.* 284, 117–132.
- Carcel D., Colombié C., Giraud F. & Courtinat B. 2010: Tectonic and eustatic control on a mixed siliciclastic–carbonate platform during the Late Oxfordian–Kimmeridgian (La Rochelle platform, western France). *Sediment. Geol.* 223, 3–4, 334–359.
- Chiarella D., Longhitano S.G. & Tropeano M. 2017: Types of mixing and heterogeneities in siliciclastic–carbonate sediments. *Mar. Petrol. Geol.* 88, 617–627.
- Coffey B.P. & Read J.F. 2007: Subtropical to temperate facies from a transition zone, mixed carbonate–siliciclastic system, Palaeogene, North Carolina, USA. *Sedimentology* 54, 2, 339–365.
- Colombié C., Schnyder J. & Carcel D. 2012: Shallow-water marl–limestone alternations in the Late Jurassic of western France: Cycles, storm event deposits or both? *Sediment. Geol.* 271, 28–43.
- Csontos L. & Vörös A. 2004: Mesozoic plate tectonic reconstruction of the Carpathian region. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 210, 1–56.
- Cuny G. 2012: Freshwater hybodont sharks in Early Cretaceous ecosystems: a review. In: P. Godefroit (Ed.): *Bernissart dinosaurs and Early Cretaceous terrestrial ecosystems*. *Indiana University Press*, Bloomington, 518–529.
- Dickson J.A.D. 1966: Carbonate identification and genesis as revealed by staining. *J. Sediment. Res.* 36, 491–505.
- Diedrich C. 2009: The vertebrates of the Anisian/Ladinian boundary (Middle Triassic) from Bissendorf (NW Germany) and their contribution to the anatomy, palaeoecology, and palaeobiogeography of the Germanic Basin reptiles. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 273, 1–16.
- Feist-Burkhardt S., Götz A.E., Szulc J., Borkhataria R., Geluk M., Haas J., Hornung J., Jordan P., Kempf O., Michalik J., Nawrocki J., Reinhardt L., Ricken W., Röhling H.-G., Rüffer T., Török Á. & Zühlke R. 2008: Triassic. In: McCann T. (Ed.): *The Geology of Central Europe*. *Geol. Soc. London*, London, 749–822.
- Ginsburg R.N. 1975: Tidal deposits. A casebook of recent examples and fossil Counterparts. *Springer-Verlag*, New York, 1–428.
- Götz A.E. & Török Á. 2008: Correlation of Tethyan and Peri-Tethyan long-term and high-frequency eustatic signals (Anisian, Middle Triassic). *Geol. Carpath.* 59, 4, 307–317.
- Götz A.E., Török Á., Feist-Burkhardt S. & Konrád Gy. 2003: Palynofacies patterns of Middle Triassic ramp deposits (Mecsek Mts., S Hungary): A powerful tool for high-resolution sequence stratigraphy. *Mitt. Ges. Geol. Berbaustud. Österr.* 46, 77–90.
- Haas J. 2001: Tisza Mega-unit. Alpine evolution. In: Haas J. (Ed.): *Geology of Hungary*. *Eötvös University Press*, Budapest, 168–193.
- Haas J. & Péro Cs. 2004: Mesozoic evolution of the Tisza Mega-unit. *Int. J. Earth. Sci.* 93, 297–313.
- Haq B.U., Hardenbol J. & Vail P.R. 1988: Mesozoic and Cenozoic chronostratigraphy and cycles of sea level change. In: Wilgus C.K. (Ed.): *Sea-level changes: an integrated approach*. *Special publication of Economic Paleontologists and Mineralogists* 42, 71–108.
- Huggett J., Cuadros J., Gale A.S., Wray D. & Adetunji J. 2016: Low temperature, authigenic illite and carbonates in a mixed dolomite-clastic lagoonal and pedogenic setting, Spanish Central System, Spain. *Appl. Clay. Sci.* 132, 296–312.
- Klappa C.F. 1980a: Rhizoliths in terrestrial carbonates: classification, recognition, genesis and significance. *Sedimentology* 27, 613–629.
- Klappa C.F. 1980b: Brecciation textures and tepee structures in Quaternary calcrete (caliche) profiles from eastern Spain: the plant factor in their formation. *Geol. J.* 15, 2, 81–89.
- Klug S., Tütken T., Wings O., Pfretzschner H.-U. & Martin T. 2010: A Late Jurassic freshwater shark assemblage (Chondrichthyes, Hybodontiformes) from the southern Juggar Basin, Xinjiang, Northwest China. *Palaeobiodiversity and Palaeoenvironments* 90, 3, 241–257.

- Kraus M.J. 1999: Paleosols in clastic sedimentary rocks: their geologic applications. *Earth. Sci. Rev.* 47, 1, 41–70.
- Lakin R.J., Duffin C.J., Hildebrandt C., Benton M.J. 2016: The Rhaetian vertebrates of Chipping Sodbury, South Gloucestershire, UK, a comparative study. *Proc. Geol. Assoc.* 127, 40–52.
- Mears E.M., Rossi V., MacDonald E., Coleman G., Davies T.G., Arias-Riesgo C., Hildebrandt C., Thiel H., Duffin C.J., Whiteside D.I. & Benton M.J. 2016: The Rhaetian (Late Triassic) vertebrates of Hampstead Farm Quarry, Gloucestershire, UK. *Proc. Geol. Assoc.* 127, 4, 478–505.
- Morsilli M., Bosellini F.R., Pomar L., Hallock P., Aurell M. & Papazzoni C.A. 2012: Mesophotic coral buildups in a prodelta setting (Late Eocene, southern Pyrenees, Spain): a mixed carbonate–siliciclastic system. *Sedimentology* 59, 766–794.
- Mutti M. & Weissert H. 1995: Triassic Monsoonal Climate and its signature in Ladinian–Carnian carbonate platforms (Southern Alps, Italy). *J. Sediment. Res.* B65, 357–367.
- Nelson S.J. 2006: Fishes of the World (4th ed.). *John Wiley & Sons Inc.*, New York, 1–601.
- Ősi A., Rabi M., Makádi L., Szentesi Z., Botfalvai G. & Gulyás P. 2012: The Late Cretaceous continental vertebrate fauna from Iharkút (western Hungary, Central Europe): a review. In: Godefroit P. (Ed.): *Bernissart dinosaurs and Early Cretaceous terrestrial ecosystems*. *Indiana University Press*, Bloomington, 532–569.
- Ősi A., Pozsgai E., Botfalvai G., Götz A.E., Prondvai E., Makádi L., Hajdu Zs., Csengődi D., Czirájk G., Sebe K. & Szentesi Z. 2013: First report of Triassic vertebrate assemblages from the Villány Hills (Southern Hungary). *Central European Geology* 56, 4, 297–335.
- Pinna G. 1990: Notes on stratigraphy and geographical distribution of placodonts. *Atti della Soc. Ital. Mus. Sciv. Stor. Nat. Milano* 131, 145–156.
- Preto N., Kustatscher E. & Wignall P.B. 2010: Triassic climates — State of the art and perspectives. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 290, 1–10.
- Pozsgai E., Józsa S., Dunkl I., Sebe K., Thamó-Bozsó E., Sajó I., Dezső J. & von Eynatten H. 2017: Provenance of the Upper Triassic siliciclastics of the Mecsek Mountains and Villány Hills (Pannonian Basin, Hungary): constraints to the Early Mesozoic paleogeography of the Tisza Megaunit. *Int. J. Earth. Sci.* 106, 6, 2005–2024.
- Rálsch-Felgenhauer E. 1985: Road-cut section in Templom Hill (Villány Hills). *Magyarország geológiai alapszelvényei*, MÁFI, Budapest, 5 (in Hungarian).
- Rálsch-Felgenhauer E. & Török Á. 1993: Mecsek and Villány Mountains. In: Haas J. (Ed.): *Triassic lithostratigraphic units of Hungary*. *Hungarian Geological Survey-MOL Ltd.* Budapest, 232–260 (in Hungarian).
- Reis H.L. & Suss J.F. 2016: Mixed carbonate–siliciclastic sedimentation in forebulge grabens: An example from the Ediacaran Bambuí Group, São Francisco Basin, Brazil. *Sediment. Geol.* 339, 83–103.
- Renesto S. 2005: A new specimen of *Tanystropheus* (Reptilia Protosauria) from the Middle Triassic of Switzerland and the ecology of the genus. *Riv. Ital. Paleontol. S.* 111, 377–394.
- Renesto S. & Dalla Vecchia F.M. 2018: Late Triassic marine reptiles. In: Tanner L.H. (Ed.): *The Late Triassic World: Earth in a Time of Transition*. *Springer Nature*, Switzerland, 263–314.
- Rieppel O. 2000: Sauropterygia I: Placodontia, Pachypleurosauria, Nothosauroida, Pistosauroida; In: Wellnhofer P. (Ed.): *Encyclopedia of Paleoherpetology*. *Verlag Dr. Friedrich Pfeil*, Munich, 1–134.
- Ruffell A. 1991: Palaeoenvironmental analysis of the late Triassic succession in the Wessex Basin and correlation with surrounding areas. *Proceedings of the Ussher Society* 7, 402–407.
- Schoch R.R. 2015: Reptilien. In: Hagdorn H., Schoch R.R. & Schweigert G. (Eds.): *Der Lettenkeuper — Ein Fenster in die Zeit vor den Dinosauriern*. *Palaeodiversity*, Munich, 231–264.
- Segesdi M., Ősi A. & Botfalvai G. 2017: New eosauroptrygian remains from the Middle Triassic of Villány, Hungary. *8th SATLW Abstracts Book*, Berlin, 47.
- Simms M.J., Ruffell A.H. & Johnson A.L. 1995: Biotic and climatic changes in the Carnian (Triassic) of Europe and adjacent areas. In: Frasnier N.C. & Sues H.D. (Eds.): *In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods*. *Cambridge University Press*, UK, 352–356.
- Stockman K.W., Ginsburg R.N. & Shinn E.A. 1967: The production of lime mud by algae in south Florida. *J. Sediment. Res.* 37, 2, 633–648.
- Török Á. 1997: Triassic ramp evolution in Southern Hungary and its similarities to Germano-type Triassic. *Acta Geol. Hung.* 40, 4, 367–390.
- Török Á. 1998: Controls on development of Mid-Triassic ramps: examples from southern Hungary. In: Wright V.R. & Burchette T.P. (Eds.): *Carbonate Ramps*. *Geological Society*, London, 149, 339–367.
- Török Á. 2000: Muschelkalk carbonates in southern Hungary: an overview and comparison to German Muschelkalk. *Zbl. Geol. Paläont.* Teil. I. 9–10, 1085–1103.
- Vörös A. 1972: Lower and Middle Jurassic formations of the Villány Mountains. *Földt. Közl.* 102, 1, 12–28 (in Hungarian).
- Vörös A. 2009: Tectonically-controlled Late Triassic and Jurassic sedimentary cycles on a peri-Tethyan ridge (Villány, southern Hungary). *Central European Geology* 52, 2, 125–151.
- Vörös A. 2010: The Mesozoic sedimentary sequences at Villány (southern Hungary). *Földt. Közl.* 140, 1, 3–30 (in Hungarian).
- Vörös A. 2012: Episodic sedimentation on a peri-Tethyan ridge through the Middle–Late Jurassic transition (Villány Mountains, southern Hungary). *Facies* 58, 415–443.
- Whiteside D.I., Duffin C.J., Gill P.G., Marshall J.E.A., Benton M.J. 2016: The Late Triassic and Early Jurassic fissure faunas from Bristol and South Wales: Stratigraphy and setting. *Paleontol. Pol.* 67, 257–287.
- Wilson J.L. 1967: Cyclic and reciprocal sedimentation in Virgilian strata of southern New Mexico. *Geol. Soc. Am. Bull.* 78, 7, 805–818.
- Wright V.P. 1994: Paleosols in shallow marine carbonate sequences. *Earth. Sci. Rev.* 35, 4, 367–395.
- Zand-Moghadam H., Moussavi-Harami R. & Mahboubi A. 2014: Sequence stratigraphy of the Early–Middle Devonian succession (Padeha Formation) in Tabas Block, East-Central Iran: Implication for mixed tidal flat deposits. *Palaeoworld* 23, 1, 31–49.
- Zeller M., Verwer K., Eberli G., Massaferrero J.L., Schwarz E. & Spalletti L. 2015: Depositional controls on mixed carbonate–siliciclastic cycles and sequences on gently inclined shelf profiles. *Sedimentology* 62, 2009–2037.

Electronic supplement

Supplement I:

Mineralogical composition based on X-Ray powder diffraction data of the Construction site

This file contains the detailed results of the X-ray powder diffraction analyses of the presented layers (beds). The results shows the mineralogical compositional changes of the presented beds indicating changes in depositional environment.

Table S1: The bulk mineralogical composition of analysed beds showing the changes in depositional environment.

Samle ID	Bulk mineralogical composition [wt. %]											
	Silicates			Carbonates				Clay minerals			anatase	goethite
	quartz	plagioclase	K-feldspar	calcite	Mg-calcite	ankerite	dolomite	10 Å phyllosilicate (muscovite/illite/biotite?)	kaolinite	swelling clays		
Layer 1	0.3			3.8			95.9					
Layer 2	3.3						82.8	5.6		7.2		1.0
Layer 5	1.8						96.5	1.7				
Layer 6	4.0			0.2			82.9	6.3		6.1		0.5
Layer 7	1.5			20.1			77.1	1.3				
Layer 7	2.7			0.2			81.5	7.4		7.6		0.6
Layer 8	12.8	0.1	2	5.8			62.1	8.3	2.1	6		0.7
Layer 9	1.5						94.5	3.1	0.9			
Layer 10_A	47.7		0.2					32.2		17.8		2.1
Layer 10_B	49.7		12.4		4.5	0.2		15.5	7.3	10.4		
Layer 10_C	58.2		11.6		0.8	0.6		15.8	5.1	7.9		
Layer 11	4.1		0.1				86.6	2.0		7.2		
Layer 12	7.9		1				55.1	24.8		8.9		2.3
Layer 13	4.4		0.5				89.2	5.9				
Layer 14	21.9		3.1	1.6			42.7	11.5	3.6	13.6		2
Layer 15_A	7.7	0.6	1.3				76.7	11.4	2.3			
Layer 15_B	3.2	0.3	0.6	0.8			93.6	1.5				
Layer 15_C	1.9	0.5		7.0			90.4	0.2				
Layer 16_A	22.8		3.1	16.7			2.4	24.3	10.8	18.8	1.1	
Layer 16_B	9.6		1.2	0.8			60.0	14.3	2.3	9.8	0.3	1.7
Layer 17_A	4.2	1.1					86.0	7.5				1.2
Layer 17_B	2.6	0.6		0.3			93.2	3.3				
Layer 18	3.7	0.8					85.7	5.6		3.4		0.8
Layer 19	3.1	0.3		0.8			88.3	3.3		4.1		
Layer 20	4.6	0.3					81.2	6.3		6.8		0.8
Layer 21	18.9	2.8		11.5			3.1	28.2	7.5	24.2	0.3	3.4
Layer 22	4.7	0.4					81.3	6.9		5.7		1.0
Layer 23	0.8	0.4		3.0			95.2	0.6				
Layer 24	2.5	0.4		3.8			90.8	2.1				0.3
Layer 26_A	4.1	0.3					89.9	2.8		2.8		
Layer 26_B	3.1	0.3					87.8	3.9		3.8		1.0
Layer 27	8.1	1.2	1.5	44.5			16.7	9.6	2.1	15.9		0.4
Layer 28	3.0	0.4		1.4			87.6	2.9		4.2		0.5
Layer 29	0.5	0.3		20.8			78.3					0.1

Supplement II:

Short summary of discovered fish remains from Triassic Villány vertebrate locality

This file contributes supplementary data to the fish faunas unearthed in the Triassic Villány vertebrate fossil sites. The data include the summarized distribution, specimen numbers and habitat preferences of the Villány fish taxa, including *Hybodus* sp., *Palaeobates angustissimus*, *Polyacrodus* sp., *Lissodus* sp., *Gyrolepis* sp., *Severnichthys acuminatus* and Actinopterygii indet..

The data shows the quantitative dominance of *Palaeobates angustissimus* in the Templomhegy Dolomite Member at the Construction site, and also that of *Hybodus* sp. in the Mészhegy Sandstone Formation at the Road-cut site. Three fish forms (*Palaeobates angustissimus*, *Gyrolepis* sp. and *Severnichthys acuminatus*) are referable to marine habitats, while *Hybodus* sp., *Polyacrodus* sp., *Lissodus* sp. and the indeterminate actinopterygian remains are less informative in paleoenvironmental point of view.

Table S2: Short summary of the discovered Villány fish remains.

Site	Formation	Age	Taxon	Description	Quantity	Paleoenvironment	References
Construction site	Templomhegy Dolomite Member	Ladinian	<i>Palaeobates angustissimus</i>	Crushing teeth; lentoid, elongated or circular occlusal view with reticulated occlusal surface	1272	marine	Dalla Vecchia & Carnevale 2011; Diedrich 2003, 2009; Pla et al. 2013; Schultze & Kriwet 1999
			<i>Lissodus</i> sp.	Low-crowned crushing teeth with sharp transversal crest and no distinctive surface sculpting	30	marine–brackish–freshwater	Cappetta 2012
			<i>Gyrolepis</i> sp.	Simple, pointed, conical teeth and thick scales with striated ganoine layer	180	marine	Allard et al. 2015; Cavicchini et al. 2018; Diedrich 2003, 2009; Landon et al. 2017; Nordén et al. 2015; Whiteside et al. 2016
			<i>Severnichthys acuminatus</i>	" <i>Saurichthys</i> "- and " <i>Birgeria</i> "-type teeth; conical teeth with fine, apicobasal striae below and on the cap	28	marine	Allard et al. 2015; Cavicchini et al. 2018; Korneisel et al. 2015; Nordén et al. 2015; Mears et al. 2016; Whiteside et al. 2016
			Actinopterygii indet.	Two different types of teeth and badly preserved, simple ganoid scales	300	marine–brackish–freshwater	Nelson 2006
	Mészhegy Sandstone Formation	Carnian	Yielded no fish fossils				
Road-cut site	Templomhegy Dolomite Member	Ladinian	Yielded no fish fossils				
	Mészhegy Sandstone Formation	Carnian	<i>Hybodus</i> sp.	Isolated cusps with apicobasal striation, circular cross-section, and smooth cutting edges	194	marine–brackish–freshwater	Cuny 2012; Dica & Codrea 2006; Klug et al. 2010 and references therein
			<i>Palaeobates angustissimus</i>	Crushing teeth; lentoid, elongated or circular occlusal view with reticulated occlusal surface	81	marine	Dalla Vecchia & Carnevale 2011; Diedrich 2003, 2009; Pla et al. 2003; Schultze & Kriwet 1999
			<i>Polyacrodus</i> sp.	Fragmentary teeth with large central cusp, well-defined lingual apron and occlusal striation	12	marine–brackish–freshwater	Böttcher 2015; Diedrich 2003, 2009; Hagdorn & Mutter 2011
			<i>Lissodus</i> sp.	Low-crowned crushing teeth with sharp transversal crest and no distinctive surface sculpting	1	marine–brackish–freshwater	Cappetta 2012
			<i>Gyrolepis</i> sp.	Simple, pointed, conical teeth and thick scales with striated ganoine layer	4	marine	Allard et al. 2015; Cavicchini et al. 2018; Diedrich 2003, 2009; Landon et al. 2017; Nordén et al. 2015; Whiteside et al. 2016
			<i>Severnichthys acuminatus</i>	" <i>Saurichthys</i> "- and " <i>Birgeria</i> "-type teeth; conical teeth with fine, apicobasal striae below and on the cap	17	marine	Allard et al. 2015; Cavicchini et al. 2018; Korneisel et al. 2015; Nordén et al. 2015; Mears et al. 2016; Whiteside et al. 2016
			Actinopterygii indet.	Two different types of teeth and badly preserved, simple ganoid scales	17	marine–brackish–freshwater	Nelson 2006

Table S3: Specimen numbers of taxa per sampled layers.

Site	Formation	Age	Taxon	Layer 22	Layer 20	Layer 18	Layer 14	Σ
Construction site	Templomhegy Dolomite Member	Ladinian	<i>Palaeobates angustissimus</i>	1	4	1	1266	1272
			<i>Lissodus</i> sp.	0	1	0	29	30
			<i>Gyrolepis</i> sp.	0	7	0	173	180
			<i>Severnichthys acuminatus</i>	0	2	0	26	28
			<i>Actinopterygii</i> indet.	2	31	4	263	300

Site	Formation	Age	Taxon	L3	L4	L5	Σ
Road-cut site	Mészhegy Sandstone Formation	Carnian	<i>Hybodus</i> sp.	3	0	191	194
			<i>Palaeobates angustissimus</i>	17	1	63	81
			<i>Polyacrodus</i> sp.	2	0	10	12
			<i>Lissodus</i> sp.	1	0	0	1
			<i>Gyrolepis</i> sp.	3	0	1	4
			<i>Severnichthys acuminatus</i>	0	0	17	17
			<i>Actinopterygii</i> indet.	2	0	15	17

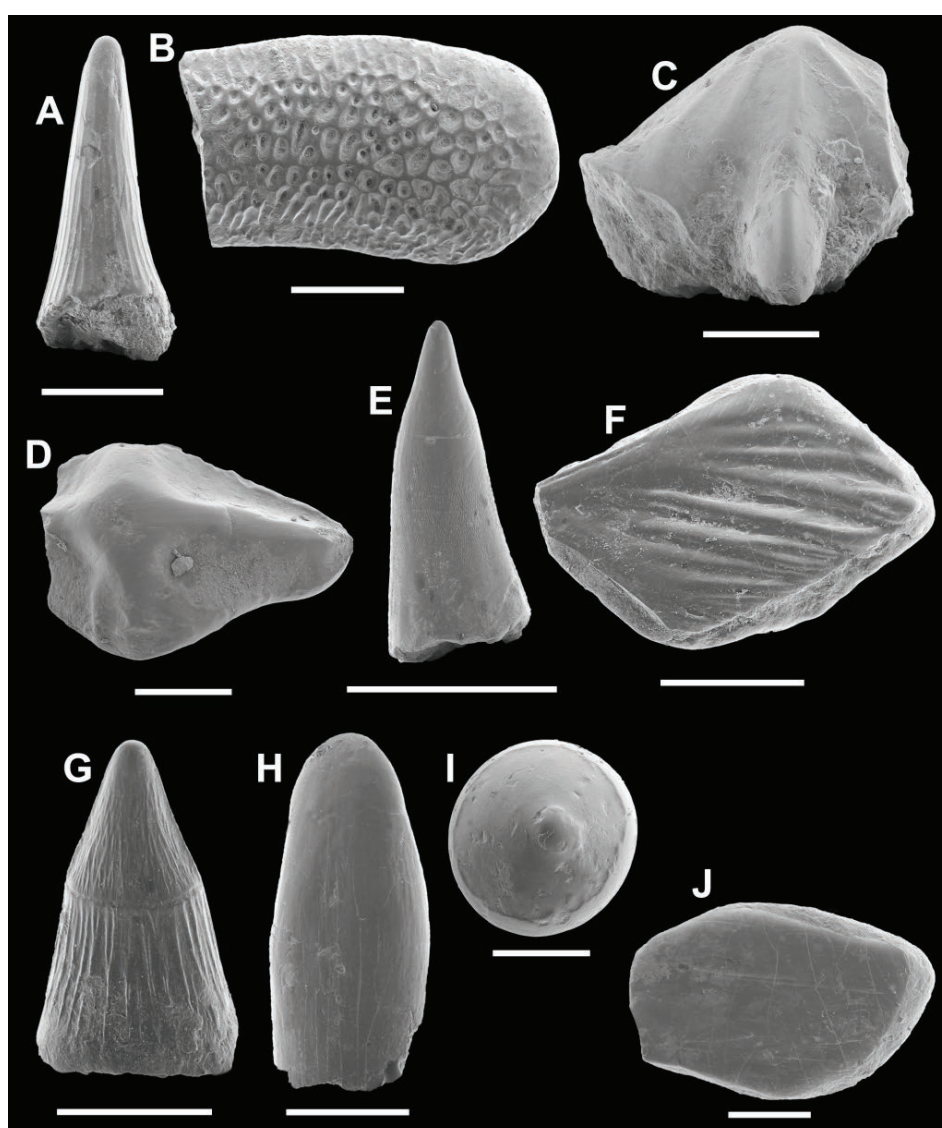


Fig. S1. Fish remains from the Villány vertebrate site. **A** — *Hybodus* sp. main cusp in lingual view. **B** — *Palaeobates angustissimus* lateral tooth in occlusal view. **C** — *Polyacrodus* sp. fragmentary tooth in labial view. **D** — *Lissodus* sp. tooth in occlusal view. **E** — *Gyrolepis* sp. tooth in profile view. **F** — *Gyrolepis* sp. scale in external view. **G** — *Severnichthys acuminatus* tooth in labial or lingual view. **H** — *Actinopterygii* indet. tooth type A in labial or lingual view. **I** — *Actinopterygii* indet. tooth type B in occlusal view. **J** — *Actinopterygii* indet. scale in external view. Scale bars: A, B, E, F, G: 1 mm; C, D, H, I, J: 500 μm.

References

- Allard H., Carpenter S.C., Duffin C. J. & Benton, M. J. 2015: Microvertebrates from the classic Rhaetian bone beds of Manor Farm Quarry, near Aust (Bristol, UK). *Proceedings of the Geologists' Association*, Doi: <http://dx.doi.org/10.1016/j.pgeola.2015.09.002>
- Cavicchini I., Heyworth H.C., Duffin C.J., Hildebrandt C. & Benton M.J. 2018: A Rhaetian microvertebrate fauna from Stowey Quarry, Somerset, U.K.. *Proceedings of the Geologist's Association*. Doi: <https://doi.org/10.1016/j.pgeola.2018.02.001>
- Dalla Vecchia F.M. & Carnevale G. 2011: Ceratodontoid (Dipnoi) calvarial bones from the Triassic of Fúsea, Carnic Alps: the first Italian lungfish. *Ital. J. Geosci.* 130, 1, 128–135.
- Dica E.P. & Codrea V. 2006: On the *Hybodus* (Euselachii) from the Early Jurassic of Anina (Caraş Severin district, Romania). *Studia Universitatis Babeş-Bolyai, Geologia* 51, 1–2, 51–54.
- Diedrich C. 2003: Die Wirbeltier-Fauna aus einer Bonebed Prospektionsgrabung in der *enodis/posseckeri*-Zone des Oberen Muschelkalkes (Unter-Ladin, Mitteltrias) von Lamerden (NW-Deutschland). *Philippia* 11, 2, 133–150.
- Hagdorn H. & Mutter R. J. 2011: The vertebrate fauna of the Lower Keuper Albertibank (Erfurt Formation, Middle Triassic) in the vicinity of Schwäbisch Hall (Baden-Württemberg, Germany). *Palaeodiversity* 4, 223–243.
- Korneisel D., Gallois R.W., Duffin C.J. & Benton M.J. 2015: Latest Triassic marine sharks and bony fishes from a bone bed preserved in a burrow system, from Devon, UK. *Proceedings of the Geologist's Association* 126, 1, 130–142.
- Landon E.N.U., Duffin C.J., Hildebrandt C., Davies T.G., Simms M. J. & Benton M.J. 2017: The first discovery of crinoids and cephalopod hooklets in the British Triassic. *Proceedings of the Geologist's Association*. Doi: <http://dx.doi.org/10.1016/j.pgeola.2017.03.005>
- Nordén K.K., Duffin C.J. & Benton M.J. 2015: A marine vertebrate fauna from the Late Triassic of Somerset, and a review of British placodonts. *Proceedings of the Geologists' Association* 126, 564–581.
- Pla C., Márquez-Aliaga A. & Botella H. 2013: The chondrichthyan fauna from the Middle Triassic (Ladinian) of the Iberian Range (Spain). *Journal of Vertebrate Paleontology* 33, 4, 770–785.
- Schultze H.-P. & Kriwet J. 1999: Die Fische der Germanischen Trias. In: Hauschke & Wilde (Eds.): Trias. Eine ganz andere Welt. Mitteleuropa im frühen Erdmittelalter. *Verlag Dr. Friedrich Pfeil*, München, 239–250.